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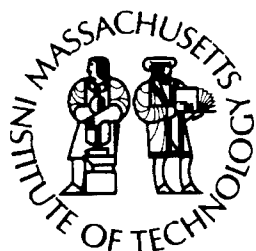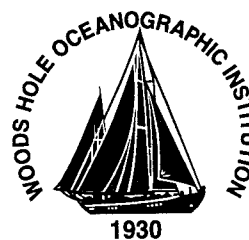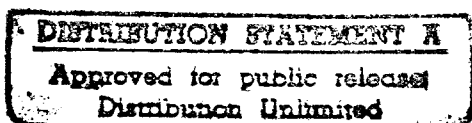
# Woods Hole Oceanographic Institution

## Joint Program in Oceanography/ Applied Ocean Science and Engineering

## DOCTORAL DISSERTATION

*Bioacoustics and Reproductive Ecology of the Damselfish* Dascyllus albisella

by

David A. Mann

September 1995

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**DOCTORAL DISSERTATION**

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# Bioacoustics and Reproductive Ecology of the Damselfish *Dascyllus albisella*

by

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B.S., Biological Sciences
Cornell University, 1988

Submitted in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

at the

Massachusetts Institute of Technology

and the
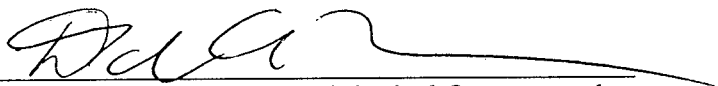
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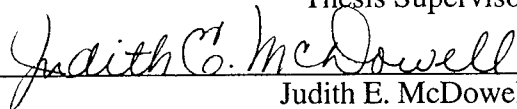
Joint Program in Biological Oceanography
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BIOACOUSTICS AND REPRODUCTIVE ECOLOGY OF THE DAMSELFISH
*DASCYLLUS ALBISELLA*

by

David A. Mann

Submitted to the Department of Biology in August 1995 in partial fulfillment of the
requirements for the Degree of Doctor of Philosophy

## Abstract

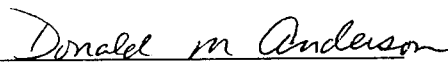While many fishes are known to produce sounds during courtship and aggression, the information contained in the sounds and their role in reproduction is not well understood. This thesis is an intensive investigation of the sounds produced by the damselfish <u>Dascyllus albisella</u>, the effect of the environment on their acoustic signals, and how the sounds relate to reproduction.

<u>D. albisella</u> males produce pulsed sounds during the signal jump, visiting by females, mating, aggression to heterospecifics and conspecifics, and nest preparation. Females make only aggressive sounds. The pulse period of aggressive sounds was shorter than courtship sounds. There was no difference between visiting and mating sounds, except in pulse duration. Two types of aggressive sounds were produced, pops and chirps. Pops were more commonly made towards heterospecifics than conspecifics. There were no differences in courtship sounds made by males from Johnston Atoll and Hawaii, except in pulse duration, which are likely due to differences in the recording environment.

The pulsed sounds produced during the signal jump of <u>D. albisella</u> were analyzed to determine what information they contain about the signal jump and how they change with propagation. There was no relationship between signal jump speed or distance with the number of pulses or pulse period of the sound. There was no consistent change in the peak frequency of pulses in a call. If echoes were present in the sound, the change in echo delay would likely have been too small for damselfish to detect. Sounds attenuated with distance such that the signal to noise ratio decreased from 17-25 dB at 1-2 m to 5-10 dB at 11-12 m. It is unlikely that <u>D. albisella</u> can detect sounds at or beyond 11-12m from the sound source, based on noise masking data from other fishes. Pulse period is least affected by propagation when compared to peak frequency, pulse duration, inter-pulse interval, and coefficient of variation of pulse amplitudes within a call. These results suggest that the sound produced during the signal jump acts over short distances and that the pulse period provides the most reliable basis for signal detection.

A passive acoustic detection system was developed to continuously record sound production activity of individual males in the field. The rate of sound production could be used to determine the timing of spawning. The daily rate of sound production increased until the day of spawning, after which it decreased by over half. Additionally, the amount of sound production at night was highest just before spawning. The passive acoustic detector also revealed that <u>D. albisella</u> had regular peaks of calling at dawn, similar to the dawn chorus in birds.

Patterns of male reproductive success varied for individual males over successive reproductive cycles and was not correlated to male size. The variation in reproductive success suggests that females choose males based on characters that vary from cycle to cycle. Data from the passive acoustic detector showed rates of courtship were positively correlated with reproductive success for three males. The continuous time-series of sound

production were analyzed to determine appropriate sampling strategies to measure male sound production over shorter time periods using SCUBA. However, short samples of sound production (10 minutes or 60 minutes per male per day) were poor estimators of peak calling rates and daily calling rates. The rich variation in male courtship rates may contain information about male condition that has been previously ignored.

Two reproductive synchrony measures were developed and used in randomization tests to test for synchronization of reproduction within five sites in the Johnston Atoll lagoon. Groups of isolated fish spawned in synchrony, but not in synchrony with other groups, even as close as 20-30 m. There was no apparent selective pressure for synchronous spawning when brood size, brood loss, and brood failure were considered. It is possible, though currently untestable, that there is a benefit of synchronous spawning for larval survival. It is unlikely that reproduction is synchronized in response to an environmental cue, because the scale of synchronization is small. Synchronization might develop through the courtship sound, because it regularly increases and decreases with spawning and the range of detectability is on the order of the range of synchronization. But, it is also possible that males are responding to chemical cues released by females. Spawning synchrony was also analyzed for 10 damselfish species. D. albisella was among the most synchronized species, along with Abudefduf troschelii. Using a phylogenetic analysis of Chromis, Amphiprion, and Dascyllus there are three viable hypotheses concerning the evolution of reproductive synchrony in D. albisella 1) it is an evolutionary relict that is no longer selected for and possibly maladaptive, 2) it evolved as part of the haremic lifestyle of the common ancestor of the Dascyllus genus, or 3) it evolved as the result of selection pressure for synchronization during the larval stage.

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# Acknowledgments

When I open anyone's thesis the first thing I look at, after unconsciously noting its thickness, is the acknowledgments. They are the most interesting to read since they tell the story of the toil that produced the thesis, and have escaped the starched formula that most scientific papers are washed with. The science cannot be understood until you understand the people that went into it.

In the acknowledgments I make a quick scan for my name. Usually it is not there. Usually it should not be there. I hope that in scanning this you find your name. If you don't, I apologize. It should be blatantly obvious that I could not have done what I did in the following pages without the help of scores of people and stealing the ideas of others that have come before me, however unintentionally. If you think something I said is new, look it up in the Origin of Species or The Descent of Man, and you shall find it there in an innocent form, free of the encumbrance of data.

My advisor, Phil Lobel, taught me all I know about field research, especially the importance of a good supply of duct tape, epoxy, and tie wraps. Judy McDowell, my co-advisor, has always been ready to help and is the best person about returning phone calls that I have ever met. Her only fault is that she never says no. Rob Fricke is unique among engineering-types in that not only is he interested in biological problems in acoustics, he entertains questions from biologists without any hint of laughter. Peter Tyack has been a fountain of knowledge, which is hard to turn off once it's on. Irv Kornfield is a mensch. I first came to WHOI (I mean the Joint Program, which for me is WHOI) to work with John Stegeman, who now serves as my chair. The great respect I have for him comes from the fact that he encouraged me to find what I was looking for when I told him I wanted to leave his lab. He did not try to convince me otherwise.

While one must thank their committee first, it is the fellow graduate students that make the process of becoming a member of the club bearable, laughable, and doable.

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Andy Solow provided a wealth of statistical advice with the reproductive synchrony work. He is the inverse of Judy McDowell when it comes to phone messages, but will buy you a box of Good n' Plenty if you make him feel guilty. I have also benefited from the generosity of other scientists with their data including Bret Danilowicz, Mike Kingsford, Vicki Tzioumis, and Chris Petersen. Steve Oliver helped at the last minute with the signal jump analysis.

The first floor of Redfield, known to people on the other floors as the basement, has a quiet community of organismal biologists. They reflect the history of the Oceanographic, and among them I found a comfortable home. Rudy and Ami Scheltema, Jim Craddock, and Rich Harbison represented what I thought WHOI should be like. They are humble, intelligent, and open.

There are plenty of behind-the-scenes folks that keep this place going: Ethel LeFave, Jane Ridge, Lisa Taylor, Colleen Hurter and the WHOI-MBL Library are the most obvious to me, but there are others who I don't even know. We all need to appreciate what they do, and where we would be without them.

Money drives science. It gets ugly when it's scarce. I have been fortunate in not having to worry about money. I was supported by the following grants to Phil Lobel: NOAA National Undersea Research Program (NOAA/NURC-FDU 89-09-NA88A-H-URD 20), the Sea Grant program at WHOI (NA86-AA-D-SG090 project R/B-97-PD), the U.S. Army Chemical Materiel Destruction Agency (via NOAA Sea Grant NA90-AA-D-SG535 and the Office of Naval Research N00014-91-J1591 and N00014-92-J-1969), the U.S. Army Legacy Resource Management Program (DAMD 17-93-J-3052), the Island Foundation and the Kelley Foundation. The Education office provided funds for travel to scientific meetings and the Copeland Family Foundation supported my connection to the internet.

I have followed the traditional acknowledgment structure, and have left my family for the end. This is wrong. My parents fueled my interest in the world when I was

growing up through innumerable trips to Beaver Lake Nature Center, Montezuma National Wildlife Refuge, and Sapsucker Woods at Cornell University. They provided so much momentum that there came a time when they didn't know what I did. Hopefully, this thesis is somewhat illuminating.

I could not have done this work without the support of my wife, Amy Donner. She didn't help because she thought the work was important, she helped because she thought the work was important to me. I could not wish for anything more. Scout, our dog, was Amy's companion during my absences and filled the void I left in the bed. Even though Scout was reluctant to give up my spot upon my return, and despite the fact that she can't read, I must thank her.

So there you have it. I don't expect you to read this thesis, unless you are working on something similar. I entreat you, though, to take the time to read the end of the Introduction and beginning of the Conclusions, for there I have reproduced some of the work of John Steinbeck that captures my philosophy. Through this thesis I 'partially' fulfill the requirements for the degree of Doctor of Philosophy. Though it is never said what the other requirements are, they are largely hoops through which I have jumped, crept, or sneaked. Now I know the secret handshake.

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# Chapter I.   Introduction

## Fish Sounds

If you have been fortunate enough to snorkel or dive on coral reefs you will know or at least have seen damselfishes. Bold males attacking and nipping in defense of their territories and nests might have surprised you. Had you stopped and listened, it would be even more surprising to hear these fish make sounds during their attack. This thesis is about the sounds made by the damselfish *Dascyllus albisella*.

Although it is not common knowledge that fishes make sounds, this fact is not new. Aristotle noted in Historia Animalium that "caprus" (possibly a *Silurus*), the "lyra" (*Trigla lyra*), and the "chalcis" (possibly *Zeus faber*) make piping sounds, the "sciaena" grunt, and one fish cuckoos (probably *T. cuculus*) (Fish and Mowbray 1970). Early studies on fish sound production are reviewed by Tavolga (1977), including work by Sorenson (1894-95) on the Siluroidae, and by Tower (1908) on drumfishes (Sciaenidae), toadfish (*Opsanus tau*), and sea-robins (*Prionotus carolinus*). Darwin (1874) speculated that "in this, the lowest class of the Vertebrata, as with so many insects and spiders, sound-producing instruments have, at least in some cases, been developed through sexual selection, as a means for bringing the sexes together."

## Phylogeny and Life Histories of Damselfishes

Damselfishes (Pomacentridae) belong to the suborder Labroidei along with cichlids (Cichlidae), wrasses (Labridae), parrotfishes (Scaridae), and surfperches (Embiotocidae) (Kaufman and Liem 1982). Sounds associated with courtship, aggression and feeding have been reported from many damselfishes (Table 1). Many cichlids have also been reported to produce pulsed aggressive and courtship sounds (Myrberg et al. 1965, Schwarz 1974, Nelissen 1977, 1978). Wrasses and parrotfishes produce sounds associated with feeding and aggression (Fish and Mowbray 1970), and hydrodynamic sounds during

spawning rushes (Lobel 1991). There have been no recordings of courtship sounds produced by wrasses and parrotfishes similar to those of damselfishes and cichlids. No sounds have been reported for surfperches. The mechanism of sound production has been hypothesized to be the grating of the pharyngeal jaws and sound amplification by the swimbladder (Fish and Mowbray 1970, Spanier 1970, Chen and Mok 1987).

There are nine members of the *Dascyllus* genus that are found from the Red Sea to the Pacific Ocean. None are found in the Caribbean or Eastern Pacific. *D. albisella* is found only in Hawaii and Johnston Atoll, while its sister species, *D. trimaculatus* is found throughout the Pacific, except at Hawaii and Johnston Atoll. *D. albisella* is among the most derived species of the genus, based on a cladistic analysis of meristic characters (Godwin in press, and D.M. unpublished data).

Stevenson (1963) published his thesis on the life history of *D. albisella* at Hawaii. Adults are found on coral heads in groups of a few to more than 100 individuals. Males guard territories where they have their nests, which consist of a cleaned area of coral. Courting males, like many other damselfish species, perform a signal jump (also known as a courtship dip). This courtship behavior is performed by rising slowly in the water column and then rapidly swimming down. Females travel between males, until they spawn in a males nest. It is not known whether they spawn in more than one nest, or return repeatedly to the same nest. Females had between 12,000-43,000 eggs at two different stages of development in their gonad simultaneously. Male nests contained between 35,000-125,000 eggs per nest, suggesting more than one female spawned in many of the nests. Males fan and guard the eggs from intruders during the four day incubation period. The eggs hatch into larvae that passively float and do not produce oriented motion, until after one to two days when they actively swim to avoid other fishes and to feed. While spawning in Hawaii occurred year round, the majority of activity occurred between May and July. After hatching the larvae leave the reef for 21 to 28 days where they complete development before settling on the reef (Booth 1991). New recruits and juveniles are

found on separate, but adjacent, coral heads from the adults (Booth 1992). *D. albisella* are not believed to change sex (J. Godwin pers. comm, Y. Sadovy pers. comm.).

*Dascyllus aruanus* is most distantly related to *D. albisella*, and the most studied *Dascyllus* species. The social structure in this species is greatly influenced by the group size. They are protogynous hermaphrodites (females change sex to males) and the male is usually the largest individual in a group (Coates 1982). At one site 38% of the fish lived in heterosexual pairs, while the rest lived in larger groups with a single male and a harem of two to six females (Fricke and Holzberg 1974). These fish are site attached; tagged individuals were rarely seen more than 1 meter from the coral where they were tagged for up to seven months (Sale 1971). However, males may move to territories where the single male of a harem had been removed (Coates 1982).

*D. aruanus* males also perform a signal jump, which was termed gamboling by Fishelson (1964). Shpigel and Fishelson (1986) reported that the dominant male uses signal swimming and sound production to dominate the other fish inhabiting the coral head. During courtship the male's black bars turn more pale. Otherwise there is no apparent difference between the sexes. Fricke and Holzberg (1974) followed two groups that spawned six times in one month. Spawning was synchronized within each group. The dominant (usually largest) female spawned first, followed by the other females in order of social rank. They did not report whether spawning was synchronized between groups. Coates (1982) suggested that there is little or no female choice of mates within a social group, and that sexual selection would act to produce males that could dominate social groups.

Shpigel and Fishelson (1986) reported an interesting situation where heterospecific groups of *D. aruanus* and *D. marginatus* were found on the same coral heads. Even in these groups with two species there was only one dominant male. As long as this fish remained the dominant male, females of the other species did not reproduce. They postulated that predation prevented individuals from moving between coral heads, and that

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predation on courting males would allow the chance for another individual to change sex into a reproductive male. In 24 cases of predation, 11 were on displaying males. Shpigel (1982) referencing the master's thesis of Avidor (1974) suggested that sound might be used as a reproductive isolating mechanism in these species. It seems likely that color would also be used, since *D. aruanus* have broad black bars, while *D. marginatus* have none.

Acoustically isolated *D. aruanus* were less aggressive than non-acoustically isolated individuals (Katzir 1981). The aggressive interactions probably control feeding success in individuals within a colony; there was a correlation between the size of prey taken and the rank in the social group (Coates 1980, Forrester 1991). Larger fish fed further upstream than smaller ones, presumably where prey was more common.

Holzberg (1973) and Fricke (1980) studied reproduction in *D. marginatus*. It was similar to *D. aruanus*, in which the sex ratio was affected by group size. The social structure in this species is greatly influenced by the size of the corals they inhabit. In small corals a single male and female may be found. On medium size corals harems of one male and two to six females are observed. On the largest coral heads and corals where there is no spacing between coral heads, there are multiple males and females. The sex ratios were 1:1 in groups with only one male and one female and in very large groups. In medium-sized groups (3-6 individuals) the largest individual was a male and the remaining individuals were all females. Males produce a sound while performing a signal jump. Males would also perform a signal jump if they were presented with another male in a bottle, indicating that this behavior was also used in aggressive interactions. Spawnings in aquaria were synchronized. All of the females on one coral colony spawned together every 9-12 days. The males mouthed, fanned, and guarded eggs for the 2-3 day incubation period. The eggs hatched 1-2 hours after sunset and the larvae drifted to the surface.

*Dascyllus reticulatus* are also protogynous hermaphrodites. Schwarz and Smith (1990) cite Wickler (1976) in describing their spawning behavior. One female may spawn

with several males. The male guards and fans the eggs 2-2.5 days (at 25 °C). If the male is prevented from fanning the eggs they develop a fungus rapidly. The courtship dip is usually only performed by males during courtship. It is sometimes executed by females or fish in sex-transition during aggressive interactions. *D. reticulatus* clearly change sex; marked individuals that spawned as females later spawned as males after the largest male was removed. Using histological examination they identified individuals as female, transitional, or male. The males either had crypts with developing spermatocytes or had abundant sperm, but not both. They interpreted this as evidence for cyclical spawning, in which spermatogenesis is completed before spawning begins, and ceases when they are actively breeding. Groups of *D. reticulatus* were found to have transformational individuals from many different dominance classes, which could still spawn as females. They suggested that these transitional individuals might migrate to corals with newly recruited fish where they would take over as head of a harem. They also noted that males had to leave corals with small interstices when they grew too large. This would also provide opportunities for transitional individuals or large females to obtain harems.

All species of *Dascyllus* that have been studied perform the signal jump. Sound production has been observed during the courtship dip for many of these species, and is likely to accompany the courtship dip all species. The studies on sound production have been mostly descriptive with no quantitative analysis of variation within and between males for different call parameters.

All of the species that have been studied can change sex, although it is seems that *D. albisella* does not. The sex ratio and social structure are influenced by coral size in *D. marginatus*. Social structure has been directly related to the ability to compete for larger food in *D. aruanus*. The social structure can influence the role of sexual selection in the mating success of different males. Sexual selection has not been investigated in any of these species. Finally, all species that have been investigated have been reported to spawn in synchrony, but the extent of synchrony and its effects has not been studied.

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## Goals of Thesis

The questions this work strives to answer about sound production and reproduction in *D. albisella* are straightforward. What kinds of sounds are made with what behavior? How are these sounds influenced by the acoustic environment? When and how often are sounds made? What information is available in the sounds about the sound-producer? What are the roles of sound in reproductive timing and mate choice?

There is great detail in the following pages and a liberal application of statistical tests. I hope in the end that the remarkable behavior of these fish is not lost among the numbers and analyses. I would be happy if they reveal more about the fish and show how much more there is to discover. As John Steinbeck wrote of his expedition to the Sea of Cortez with Ed Ricketts:

"We were curious. Our curiosity was not limited, but was as wide and horizonless as that of Darwin or Agassiz or Linnaeus or Pliny. We wanted to see everything our eyes would accomodate, to think what we could, and, out of our seeing and thinking, to build some kind of structure in modeled imitation of the observed reality. We knew that what we would see and record and construct would be warped, as all knowledge patterns are warped, first, by the collective pressure and stream of our time and race, and second by the thrust of our individual personalities. But knowing this we might not fall into too many holes--we might maintain some balance between our warp and the separate things, the external reality. The oneness of these two might take its contribution from both. For example: the Mexican sierra has "XVII-15-IX" spines in the dorsal fin. These can be easily counted. But if the sierra strikes hard on the line so that our hands our burned, if the fish sounds and nearly escapes and finally comes in over the rail, his colors pulsing and his tail beating in the air, a whole new relational externality has come into being--an entity which is more than the sum of the fish plus the fisherman. The only way to count the spines of the sierra unaffected by this second relational reality is to sit in a laboratory, open an evil-smelling jar, remove a stiff colorless fish fom formalin solution, count the spines, and write the truth "D. XVII-15-IX." There you have recorded a reality which cannot be assailed--probably the least important reality concerning either the fish or yourself."

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Table I. Sound producing damselfishes and behavior associated with sound production.

| Species | Description of Sound | Reference |
|---|---|---|
| *Amphiprion clarkii* | Pop and chirp (agonistic) | Chen and Mok (1987) |
| *Amphiprion frenatus* | Chewing and agonistic | Schneider (1964) |
| *Amphiprion frenatus* | Pop and chirp (agonistic) | Chen and Mok (1987) |
| *Amphiprion percula* | Chewing and agonistic | Schneider (1964) |
| *Amphiprion polymnas* | Chewing and agonistic | Schneider (1964) |
| *Amphiprion xanthus* | Chewing and agonistic | Schneider (1964) |
| *Dascyllus aruanus* | Courtship | Avidor (1974) |
| *Dascyllus carneus* | ? | Koenig, 1957 (as cited by Randall and Allen, 1977) |
| *Dascyllus marginatus* | Courtship | Avidor (1974) |
| *Dascyllus marginatus* | Courtship | Holzberg (1973) |
| *Dascyllus trimaculatus* | Chewing, agonistic, courtship | Spanier (1970) |
| *Dascyllus trimaculatus* | Pop and chirp (agonistic) | Luh and Mok (1986) |
| *Hypsypops rubundica* | Thumping noises as males rush females | Limbaugh (1964) |
| *Microspathodon chrysurus* | Knocking sounds by males when touched by diver | Emery (1968) |
| *Pomacentrus nagasakiensis* | Enticement grunting sounds as male rushes towards female | Moyer (1975) |
| *Stegastes dorsopunicans* | Courtship | Spanier (1979) |
| *Stegastes fuscus* | Courtship | Myrberg (1972) |
| *Stegastes leucostictus* | Courtship | Spanier (1979) |
| *Stegastes partitus* | Agonistic, courtship | Myrberg (1972) |
| *Stegastes partitus* | Courtship | Spanier (1979) |
| *Stegastes planifrons* | Courtship | Spanier (1979) |
| *Stegastes variabilis* | Courtship | Myrberg (1972) |

# Chapter II


# Sounds of the Damselfish *Dascyllus albisella*

# Abstract

Dascyllus albisella males produce pulsed sounds during the signal jump, visiting by females, mating, aggression to heterospecifics and conspecifics, and nest preparation. Females make only aggressive sounds. The pulse period of aggressive sounds was shorter than courtship sounds. There was no difference between visiting and mating sounds, except in pulse duration. Two types of aggressive sounds were produced, pops and chirps. Pops were more commonly made towards heterospecifics than conspecifics. There were no differences in courtship sounds made by males from Johnston Atoll and Hawaii, except in pulse duration. The differences in pulse duration are likely due to differences in the recording environment.

# Introduction

Damselfishes (Pomacentridae) are prolific sound-producers. Most studies of damselfish sound production have been performed with members of the Stegastes genus, with the most detailed description of Stegastes partitus (Myrberg, 1972; Ha, 1973; Spanier, 1979; Myrberg et al., 1986). The sounds of four congeneric Stegastes spp. could be distinguished by each species based on pulse period and the number of pulses in a call, although the discrimination was not perfect (Spanier 1979).

Species-specific sounds are important as mating isolation mechanisms in insects and frogs (Ewing, 1989; Wells and Henry, 1992; Ryan and Rand, 1993). The temporal structure of their pulsed sounds is the most variable between species and an important component of species recognition (Ewing, 1989; Wells and Henry, 1992; Cocroft and Ryan, 1995). While there is variation in the sounds produced by damselfishes and cichlids (Cichlidae), their role in mating isolation is not understood (Myrberg et al., 1965; Nelissen, 1977; Nelissen, 1978; Spanier, 1979).

The goal of this paper is to completely describe the sounds produced by the damselfish Dascyllus albisella, and compare those made by fishes at Johnston Atoll and Hawaii, which are separated by 850 km. We have previously described the courtship and mating sounds and the relationship of male size to the dominant frequency of courtship sounds (Lobel and Mann, in press). This paper adds an analysis of several other sounds, as well as a signal analysis procedure that can be consistently applied to all of these signals, as well as similar sounds produced by other fishes.

## Methods and Materials

### Recordings

Field recordings of sound production by <u>D. albisella</u> were made using SCUBA at Johnston Atoll, Central Pacific Ocean (16° 44.2' N, 169° 31.0' W) in April 1994 and at Kaneohe Bay, Oahu, Hawaii (21° 27'N, 157° 47'W) in May 1992. Sounds were recorded using a hydrophone coupled to a SONY V-9 8-mm Handycam in an underwater housing. The hydrophone was attached to a float and affixed to a 2 m boom so that it floated 0.5m off the bottom. Recordings were made with fish approximately 1-2 m from the hydrophone. Recordings at Johnston Atoll were made in approximately 4m depth water on a flat bottom, and recordings at Hawaii were made at 3-4 m depth on a bottom that sloped to 10 m.

### Signal Analysis

Sounds and their associated behavior were analyzed by playing the video to observe behavior and digitizing the audio at 10 kHz using the computer program SIGNAL (Engineering Design). Acoustic measurements were made using an automatic detection algorithm, as opposed to manually to avoid user bias. The following steps in signal analysis are illustrated in figure 1. Signals were low-pass filtered at 1000 Hz. The resulting signal was divided by its rms amplitude, rectified, an envelope function was calculated using a 3 msec decay, then the signal was smoothed with a 3 msec window. Individual pulses were detected by gating the signal, which determines the on- and off-times of pulses by comparing the pulse amplitude to a threshold value. The threshold was dynamically defined for each signal as the maximum noise level in the first 20 msec plus 20% of the maximum signal amplitude (after rectification, envelope, and smoothing). From these detected signals pulse number, pulse duration, inter-pulse interval (IPI), pulse period (number of msec per pulse), and coefficient of variation (CV) of pulse amplitude

within a call, were calculated (see fig.1 for a definition of each of these). Peak frequency for each pulse of a call was calculated with an n-point FFT and a Hanning window (where n was the next highest power of 2 of the number of points in the digitized signal). Frequency envelopes were calculated as the difference in frequencies 3dB less than the peak frequency.

# Results

## Effect of SNR on Analysis

The signal to noise ratio (SNR) of sounds could affect measurements of the on- and off-times of pulses. If the error were constant, then it might be possible to correct the measurements depending on the SNR. This was empirically tested by adding random noise to eight courtship signals with a high SNR, and measuring the change in pulse duration at different SNRs (Fig. 2). The coefficient of determination of the regression of SNR on the change in duration was 0.275, which indicated that it would not be possible to accurately determine pulse on- and off-times using the SNR. However, there was less than 1 msec variation in pulse duration at SNRs greater than 18 dB. Therefore, only signals with SNR>18 dB were used in the sound analysis of pulse duration and IPI.

## Description of Sounds

Sounds were produced by males during the signal jump, visiting by females, mating, aggression, and nest cleaning (Fig. 3). Females produced sounds only during aggression. The signal jump consisted of a male rising in the water column and then rapidly swimming

down while making a sound. The visiting sound was produced by males when females visited the nests that males have prepared prior to spawning. Males and females performed a pseudo-spawning behavior during visiting, with both passing over the nesting surface. The visiting sound was produced as the male quivered his body. The behavior is the same as that during actual spawning (Lobel and Mann in press). The aggressive sounds were produced when chasing other D. albisella or other fishes. Females produced aggressive sounds when chasing juveniles. Not all chases by males or females are accompanied by sound production. The nest picking sound was heard from one male when he was preparing his nest prior to spawning, and occurred as he bit at the substrate.

Each of the sounds were compared using the data from Johnston Atoll for the number of pulses (Fig. 4), pulse period (Fig. 5), IPI (Fig. 6), pulse duration (Fig. 7), and CV of pulse amplitudes (Fig. 8). The aggressive sounds were statistically compared to the courtship (signal jump) sounds, and there were significant differences in all call characteristics, except frequency envelope (Table 1). The mating sounds were compared to the visiting sounds, and only pulse duration was statistically different (Table 2).

Two types of aggressive sounds were produced: a popping sound that was either one or two pulses, and a chirp resembling the courtship sound. One and two-pulse aggressive sounds were made more often to heterospecific fishes (including the boxfish Ostracion meleagris, the butterflyfishes Chaetodon trifasciatus and Forcipiger flavissimus, the surgeonfish Ctenochaetus strigosus, and the wrasses Epibulus insidiator and Cheilinus unifasciatus) and pestering divers (Homo sapiens), than to conspecifics (p-value<0.0001; Mann-Whitney U comparing number of pulses in aggressive sounds to heterospecifics and conspecifics) (Fig. 9). Multiple-pulse chirps were more often made towards conspecifics. It is important to note that both pops and chirps were made to hetero- and conspecifics (Fig 9). The pop and the chirp sound different to the human ear, however there was no significant difference in average pulse duration of pops versus chirps (p=0.188; one-way ANOVA), and there was no difference in peak frequency (p=0.787; paired t-test of average

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frequencies for each sound type; n=6 males). On two occasions there was an aggressive interaction between a male D. albisella and a male Ostracion meleagris, during which both made sounds (Fig. 10). D. albisella made an aggressive pop and O. meleagris produced a tonal sound.

The first pulse of the courtship sound seemed shorter than the other pulses (Fig. 3). The duration of each pulse was compared to the others in paired t-tests, and histograms of the ratio of pulse durations were plotted (Fig. 11). The first pulse was significantly shorter than all other pulses, and there was generally an increase in pulse duration from first to last. It is important to note that the first pulse was not always the shortest (Fig. 10).

The pulse period of a call could be influenced by changing pulse duration and/or IPI. To determine which was important, pulse duration and IPI of courtship and aggressive sounds were regressed against pulse period (Fig. 12). The slopes for IPI were significantly different than zero for both courtship and aggressive sounds (p<0.001). The slopes for pulse duration were not statistically different than zero for either courtship (p=0.386) or aggressive (p=0.129) sounds.

## Johnston Atoll and Hawaii

The courtship sounds made by D. albisella at Johnston Atoll and Hawaii were compared (Fig. 13). Only pulse duration was significantly different for the two sites; the average at Johnston Atoll was 1.6 msec greater than at Hawaii (Table 3).

## Discussion

Dascyllus albisella males produce pulsed sounds during the signal jump, visiting by females, mating, aggression to heterospecifics and conspecifics, and nest preparation. Females make only aggressive sounds. There were differences among the sounds in pulse

number and pulse period (through changes in IPI), but they all had overlapping distributions. The signal jump sound functions as a courtship sound, since the rate of signal jumping increases during visiting and mating (Mann and Lobel, in press). It also may function as a territorial signal, since it is produced at other times when females are feeding and outside of the reproductive season (Mann and Lobel in press). This dual function of the signal jump is supported by experiments with Dascyllus aruanus in which males started the signal jump when exposed to other males in bottles (Holzberg, 1973). The visiting and mating sounds may also act as courtship sounds. The nest picking sounds are most likely incidental, without communicative purpose.

The difference in aggressive sounds made to heterospecifics versus conspecifics shows that D. albisella can discriminate other species from themselves. While this is no great discovery, the acoustic aggressive interaction between D. albisella and the boxfish O. meleagris is the first reported sonic interaction between two fish species. The sound made by O. meleagris is similar to that reported for trunkfish (Ostraciidae) (Fish and Mowbray, 1970).

The first pulse of the courtship and aggressive sounds was usually shorter than the other pulses. This probably reflects a property of the mechanism of sound production, in which the state of the swimbladder or percussive force on it is in a different position for the first pulse as the following pulses.

There was no difference in the sound made during the signal jump by D. albisella at Johnston Atoll and Hawaii, except for a difference in pulse duration. The difference in pulse duration is likely due to differences in the recording environments at the two sites (see Chapter 3). The courtship sound of Dascyllus trimaculatus from the Red Sea (Israel) and the Pacific Ocean (Japan), has the same number of pulses and pulse period as D. albisella, although there are not extensive data on the distributions of these call characteristics (Spanier, 1970; Luh and Mok, 1986). D. albisella is found only at Johnston Atoll and Hawaii, while D. trimaculatus has a broad distribution in the Pacific and Red Sea,

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but it is not found at Johnston Atoll or Hawaii (Randall and Allen, 1977). This reveals that the sound is probably not learned, and that it has evolved slowly in D. trimaculatus and D. albisella and has not been important in the speciation of D. albisella.

There are species differences, in pulse number and pulse period, in the sounds made by other damselfishes, cichlids, and sunfishes (Gerald, 1971; Nelissen, 1977; Nelissen, 1978; Spanier, 1979). Thus, sounds may function as a premating isolating mechanism in some of these fishes as they do in some frogs and insects (Ewing 1989, Ryan and Rand 1993). However, the ability of fishes to detect differences in pulse period is not highly acute. Goldfish can only detect changes of 10 msec in pulse periods of 40 msec (Fay, 1982b). While the discrimination abilities of fishes that make pulsed sounds might be better, the results of discrimination experiments with four Stegastes spp. suggest that at most they can detect 5 msec differences in pulse period (Myrberg *et al.* 1978; Spanier 1979). Psychophysical experiments are needed to measure their sensitivity to differences in pulse number and pulse period to determine its potential importance in mating isolation (Fay, 1982a).

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Chrysopidae). Evol. 46: 31-42.

Table 1. Comparison of courtship and aggressive sounds. P-values are the results of Mann-Whitney U Tests for pulses, IPI, period, pulse duration, CV Amp. P-values for frequency and frequency envelope used 2-way ANOVAs with call type (aggressive and courtship) and individual (5 males) as factors; the p-values shown are for differences in call type.

| | Aggressive | | Courtship | | p-value |
|---|---|---|---|---|---|
| | n | mean | n | mean | |
| Pulses | 50 | 4.8 | 185 | 5.3 | 0.034 |
| IPI | 44 | 29.2 | 113 | 40.3 | <0.001 |
| Period | 47 | 44.5 | 184 | 52.9 | <0.001 |
| Pulse Duration | 48 | 15.2 | 143 | 12.9 | <0.001 |
| Frequency | 48 | 441.8 | 48 | 371.2 | 0.032 |
| Frequency Envelope | 143 | 145.7 | 143 | 156.2 | 0.075 |
| CV Amplitude | 47 | 0.18 | 184 | 0.26 | <0.001 |

Table 2. Comparison of visiting and mating sounds. P-values are from Mann-Whitney U Tests.

| | Mating | | Visiting | | p-value |
|---|---|---|---|---|---|
| | n | mean | n | mean | |
| Pulses | 103 | 2.8 | 67 | 3.0 | 0.083 |
| IPI | 38 | 42.5 | 40 | 45.8 | 0.382 |
| Period | 103 | 78.7 | 63 | 55.8 | 0.095 |
| Pulse Duration | 66 | 14.1 | 47 | 12.5 | <0.001 |
| CV Amplitude | 88 | 0.24 | 63 | 0.22 | 0.844 |

Table 3. Comparison of courtship sounds from Johnston Atoll and Hawaii. P-values are the results of a Kolmogorov-Smirnov test of differences between distributions. Only pulse duration is statistically significantly different at the two sites.

| | Johnston Atoll | | | Hawaii | | | p-value |
|---|---|---|---|---|---|---|---|
| | n | mean | SD | n | mean | SD | |
| Pulses | 335 | 5.5 | 1.2 | 64 | 5.7 | 1.2 | 0.211 |
| IPI | 118 | 38.4 | 6.6 | 39 | 36.2 | 7.2 | 0.088 |
| Period | 334 | 53.0 | 6.6 | 63 | 46.1 | 7.8 | 0.500 |
| Duration | 118 | 14.0 | 3.2 | 46 | 12.4 | 2.0 | 0.011 |
| CV amp | 334 | 0.25 | 0.15 | 64 | 0.27 | 0.11 | 0.110 |

Figure 1. Signal analysis of the sound produced during the signal jump. The original signal is shown in the bottom panel (panel 1) after low-pass filtering. The signal is then rectified and its envelope calculated with a 3 msec decay time (panel 2). After smoothing with a 3 msec window (panel 3) the signal is gated to determine on-times (amplitude of 1) and off-times (amplitude of 0) of the pulses. The characteristics measured from the gated signal are shown in panel 4.

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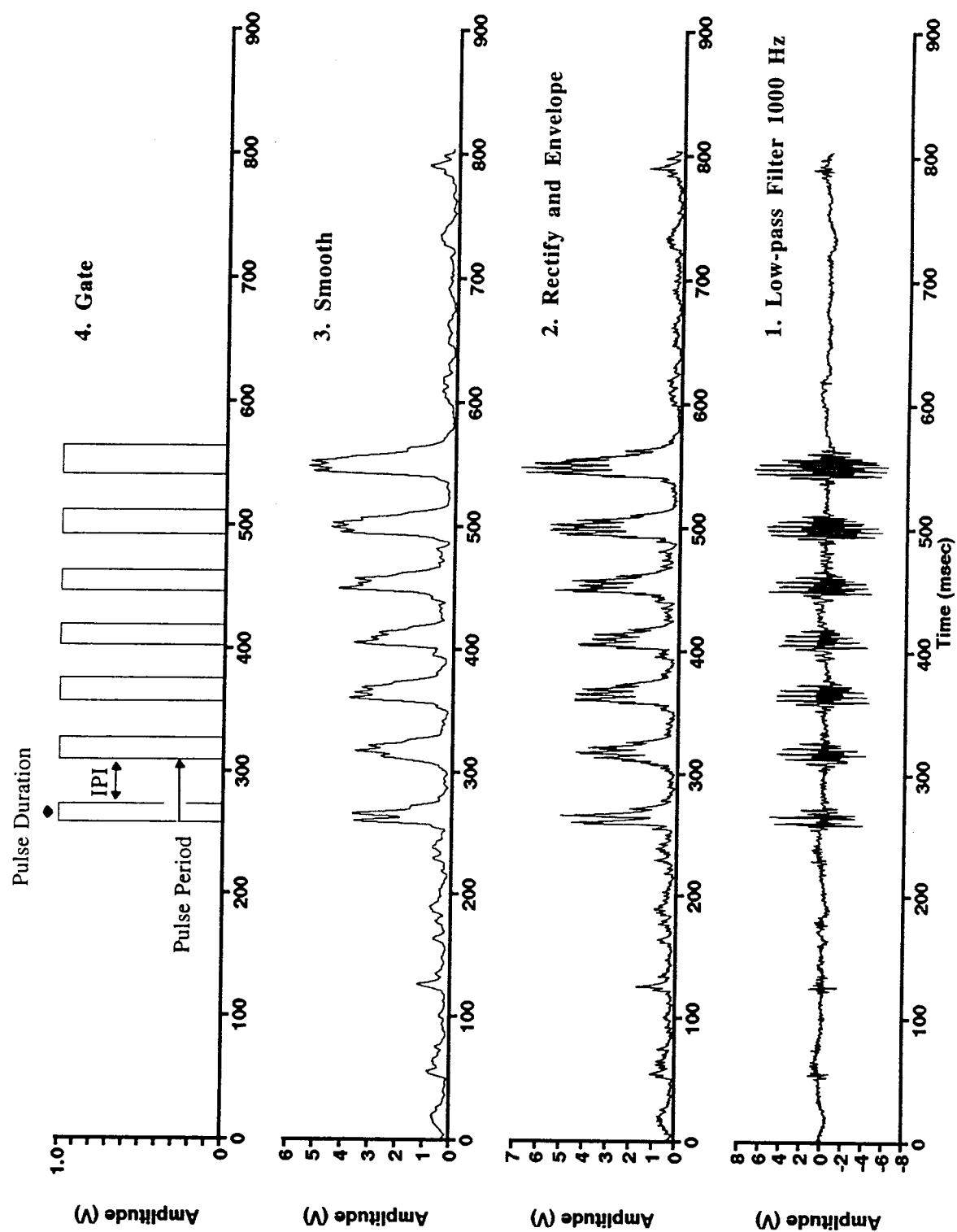
Figure 2. Effect of SNR on the measured pulse duration (duration with no added noise-duration with added noise). A. Change in duration for each pulse in a call. B. Mean (square) and 1 standard deviation (error bars) of changes in duration for all of the pulses at each SNR.

**A.** $y = 259.976x^{-2.019}$   $r^2 = 0.275$

Pulse 1
Pulse 2
Pulse 3
Pulse 4
Pulse 5
Pulse 6
Pulse 7

**B.**
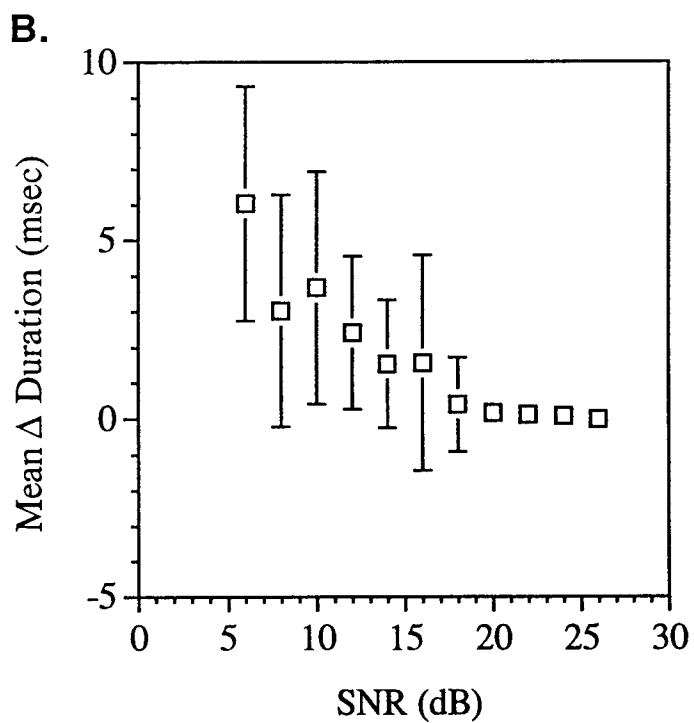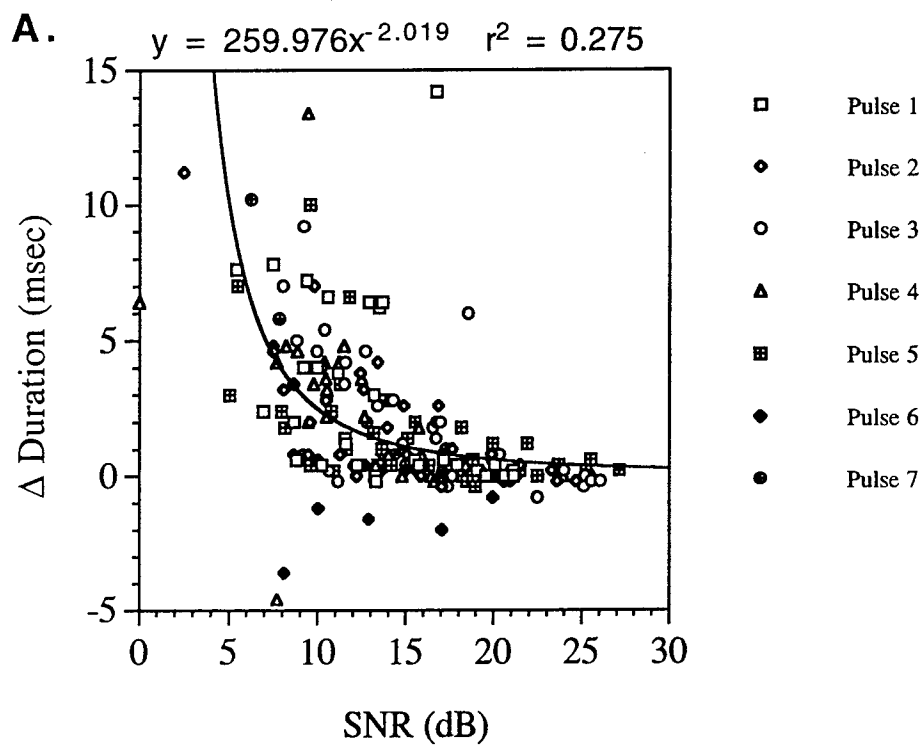
Figure 3. Oscillograms of the sounds produced by male *D. albisella*.
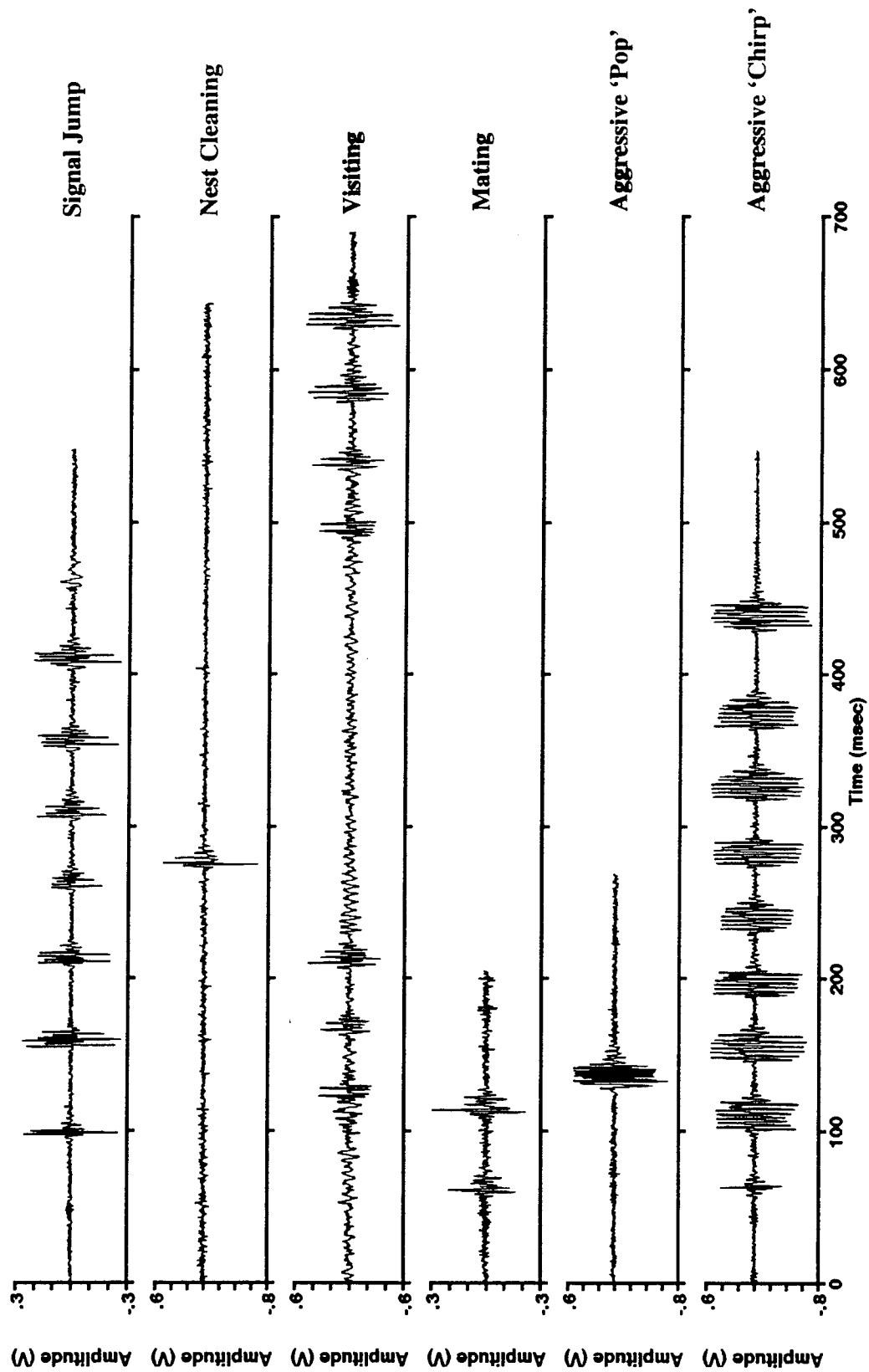
Figure 4.  Histograms of the number of pulses in the sounds produced by *D. albisella*.
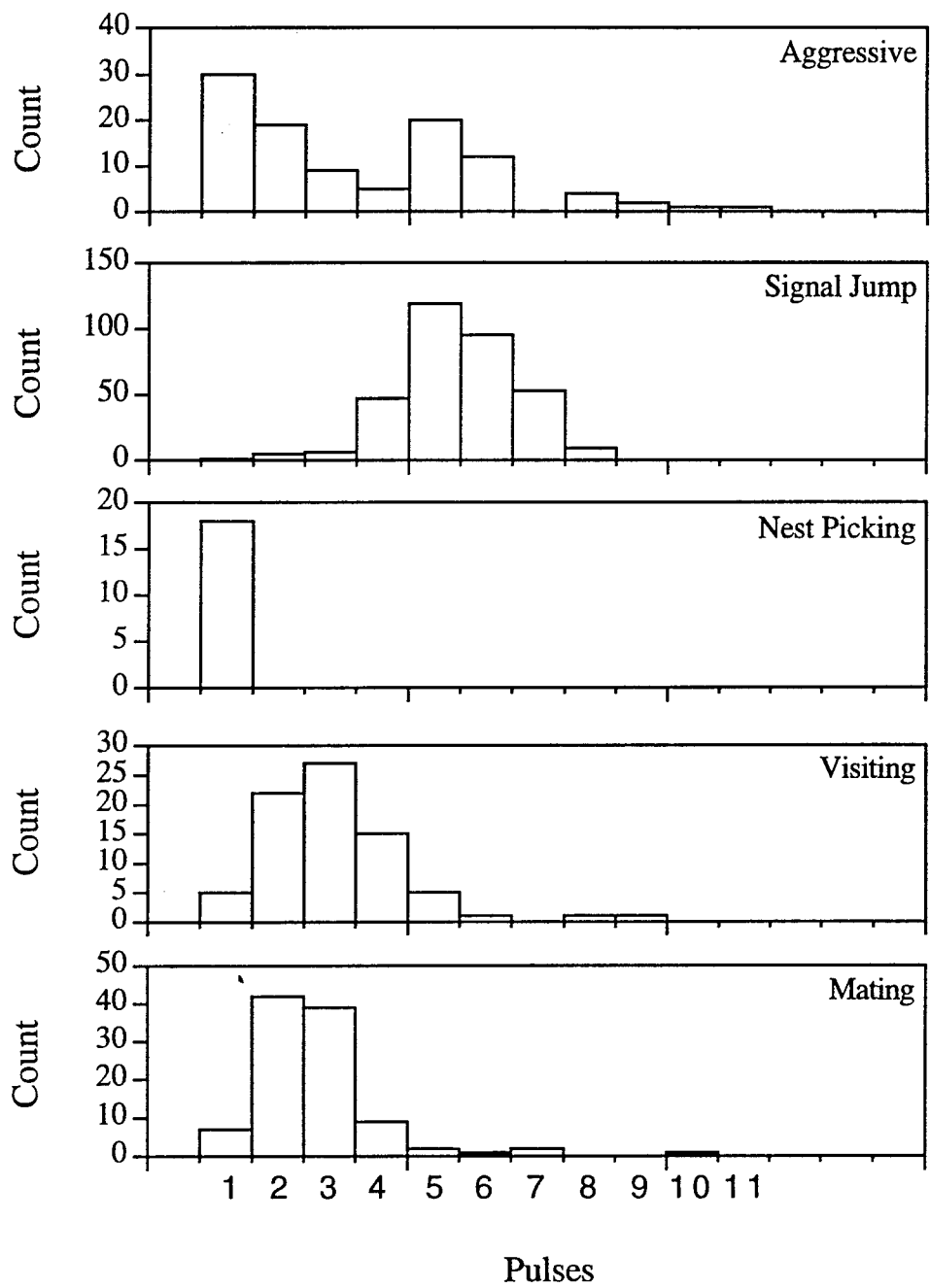
Figure 5. Histograms of the pulse period of the sounds produced by *D. albisella*.
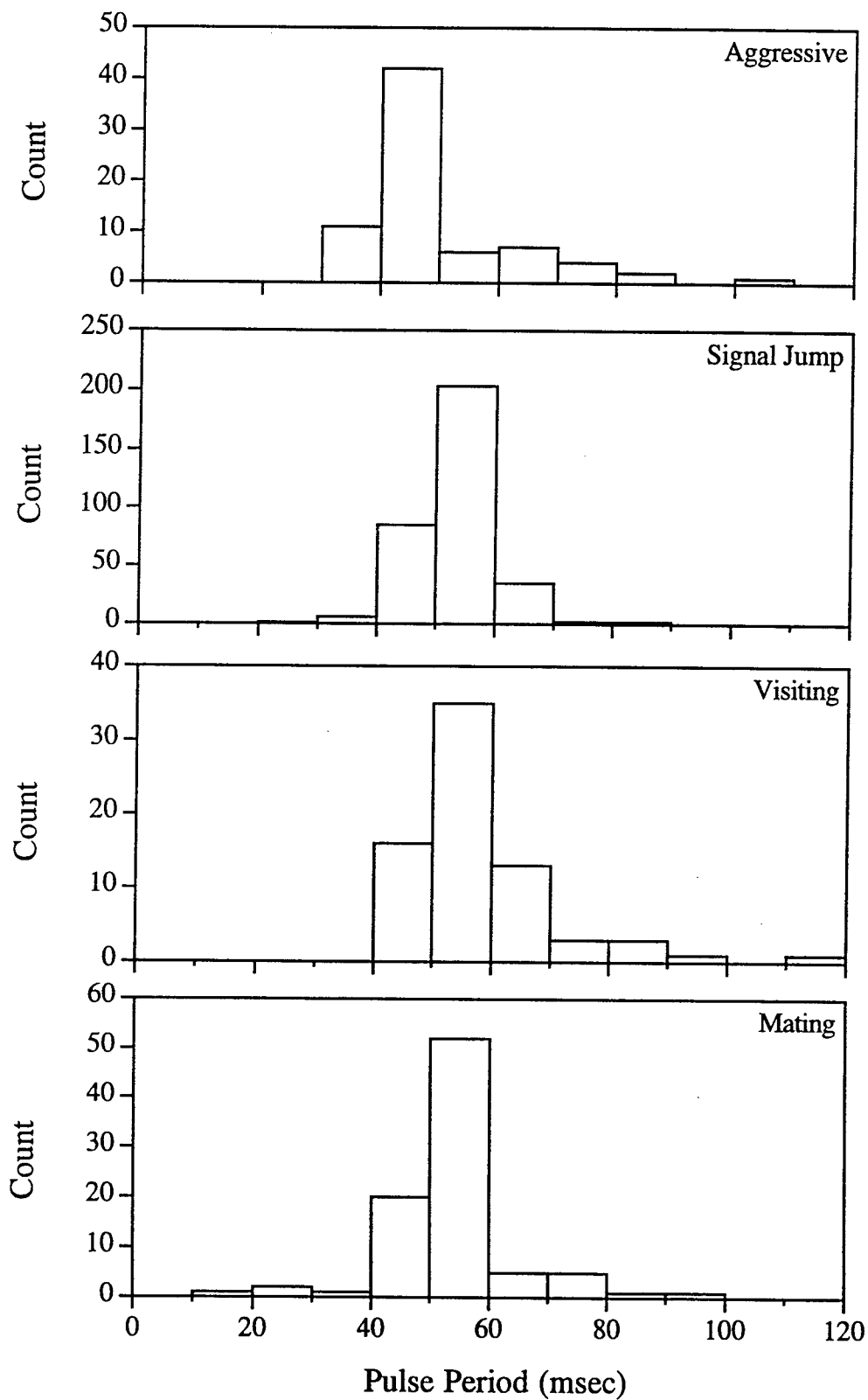
Figure 6. Histograms of the inter-pulse interval (IPI) in the sounds produced by *D. albisella.*
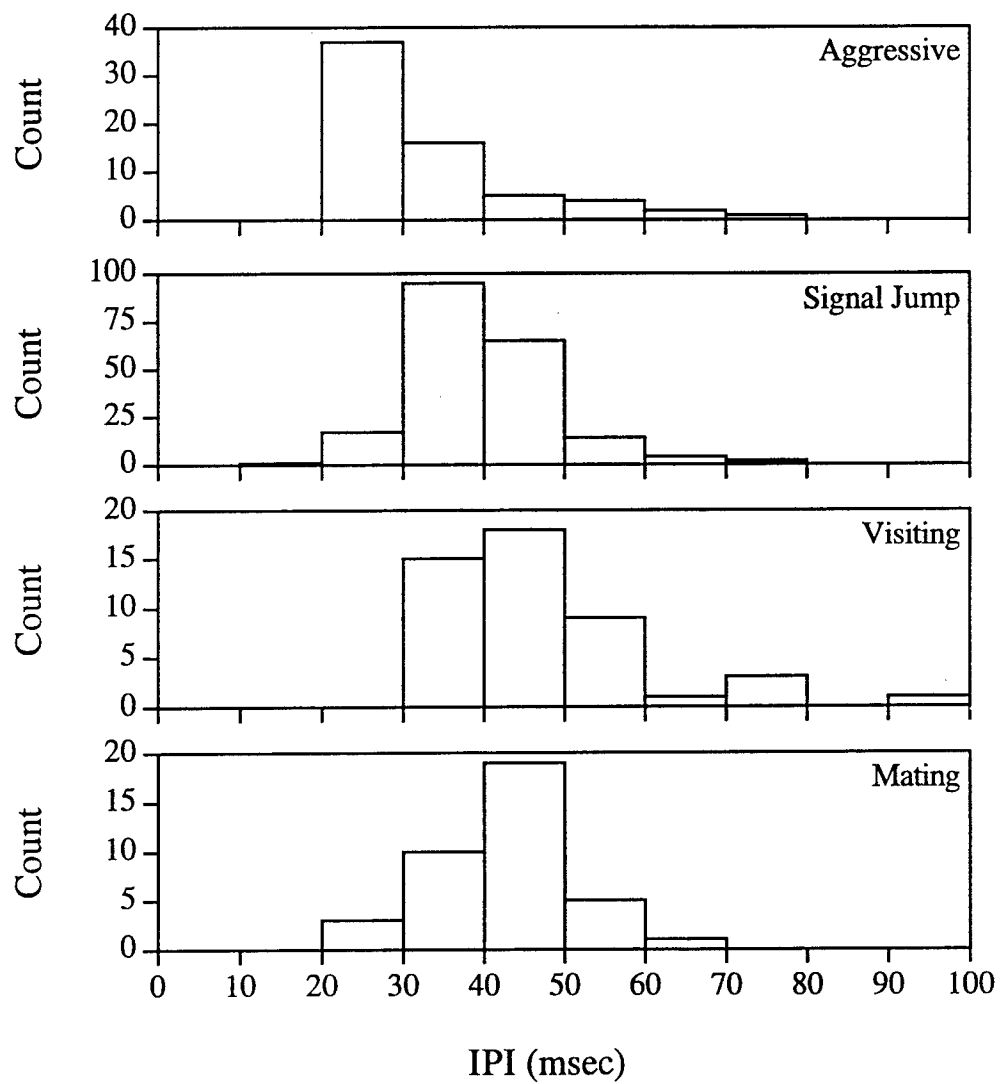
Figure 7. Histograms of the pulse duration in the sounds produced by *D. albisella*.
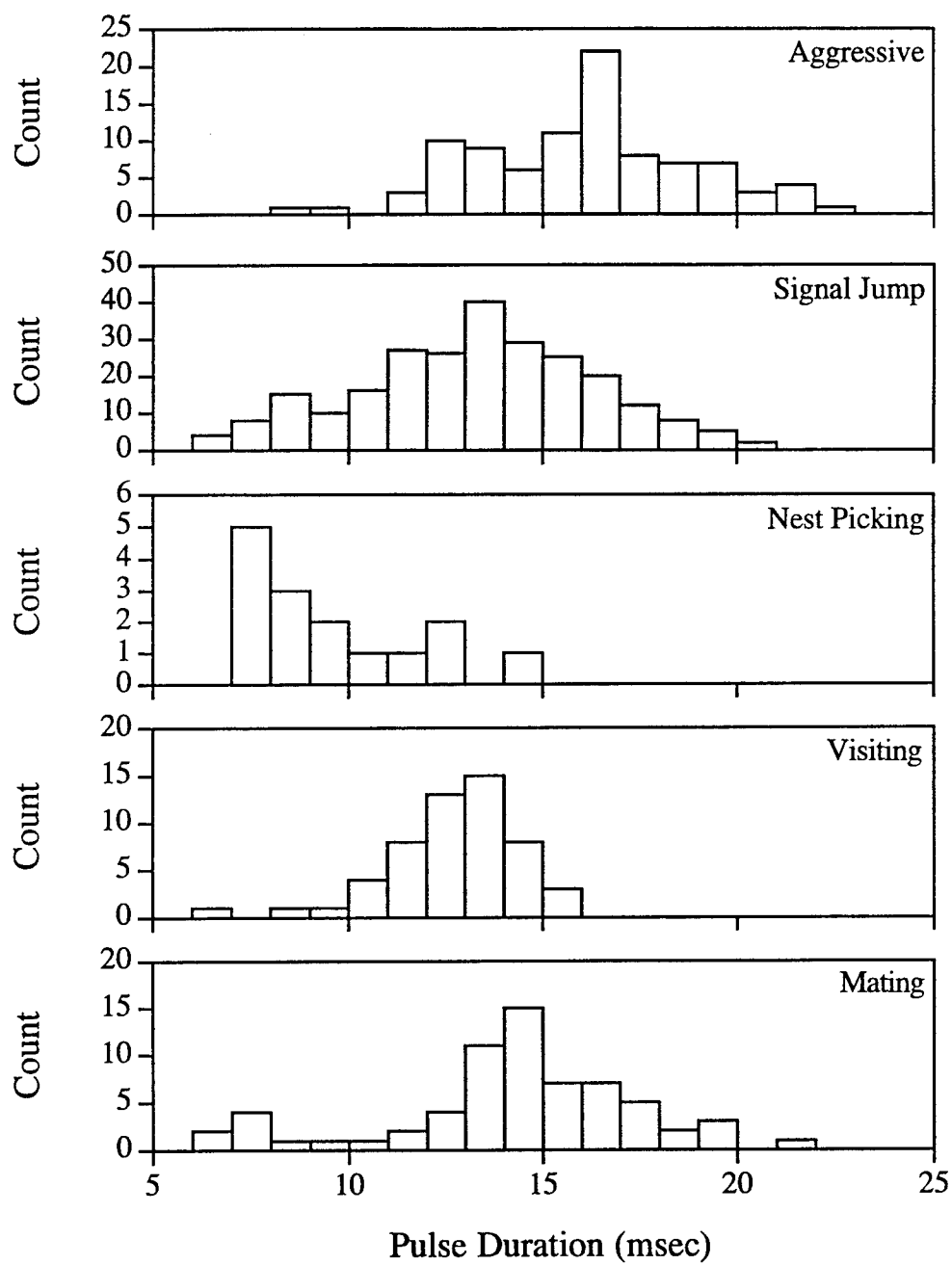
Figure 8. Histogram of the coefficient of variation (CV) of pulse amplitudes within a sound
for the sounds produced by *D. albisella*.
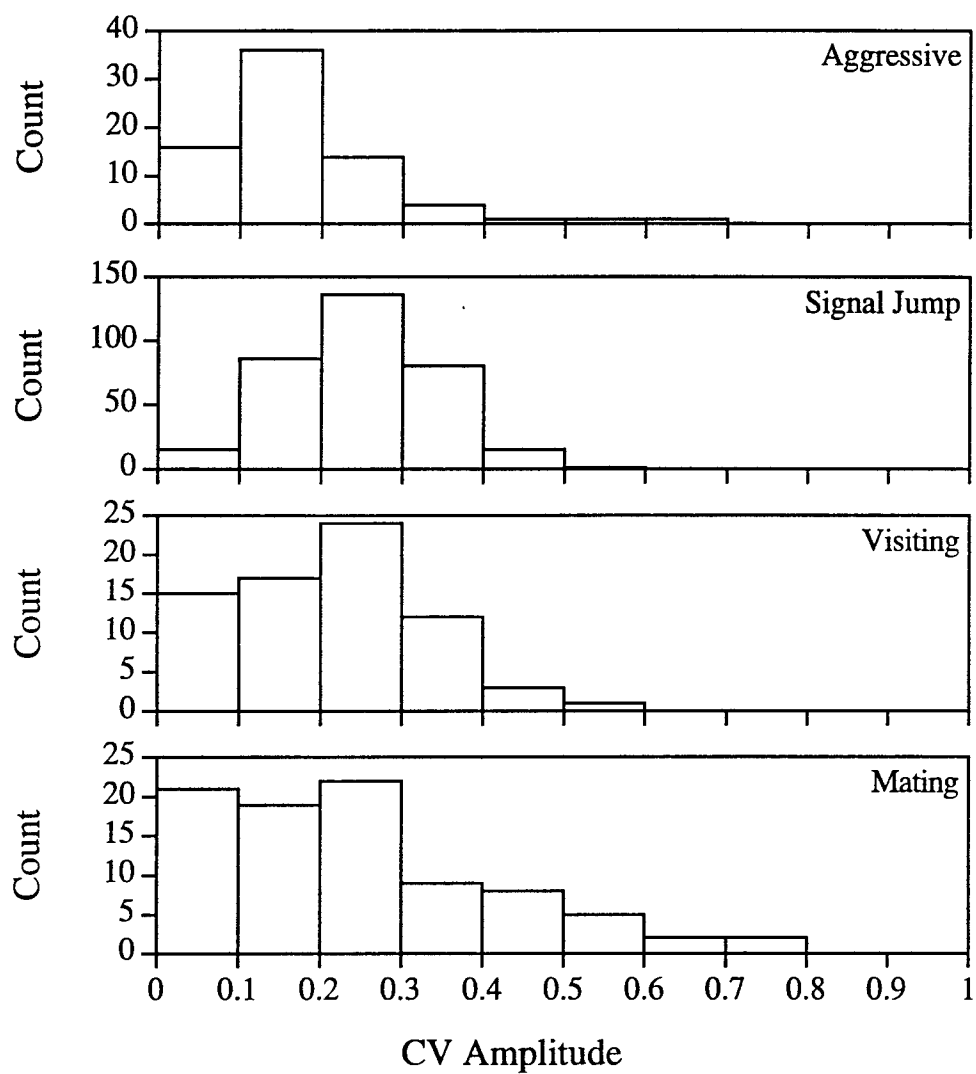
Figure 9. Histograms of the number of pulses in aggressive sounds. The first three

histograms are based on the object of male aggression. The bottom histogram is based on

female aggression to smaller *D. albisella*.
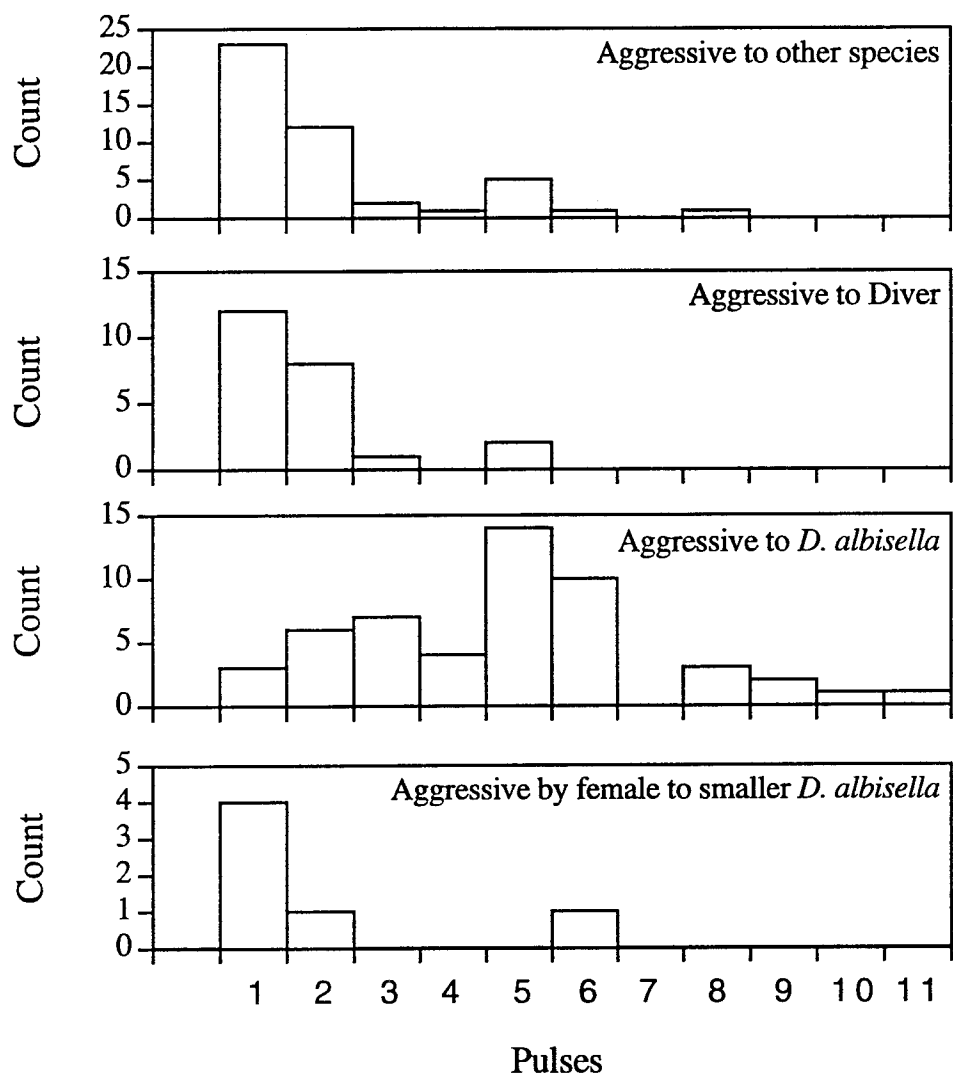
Figure 10. Oscillogram (above) and sonograph (below) of an aggressive interaction between a male *D. albisella* and a male boxfish *Ostracion meleagris*. The pop is produced by *D. albisella* and the tone is produced by *O. meleagris*.
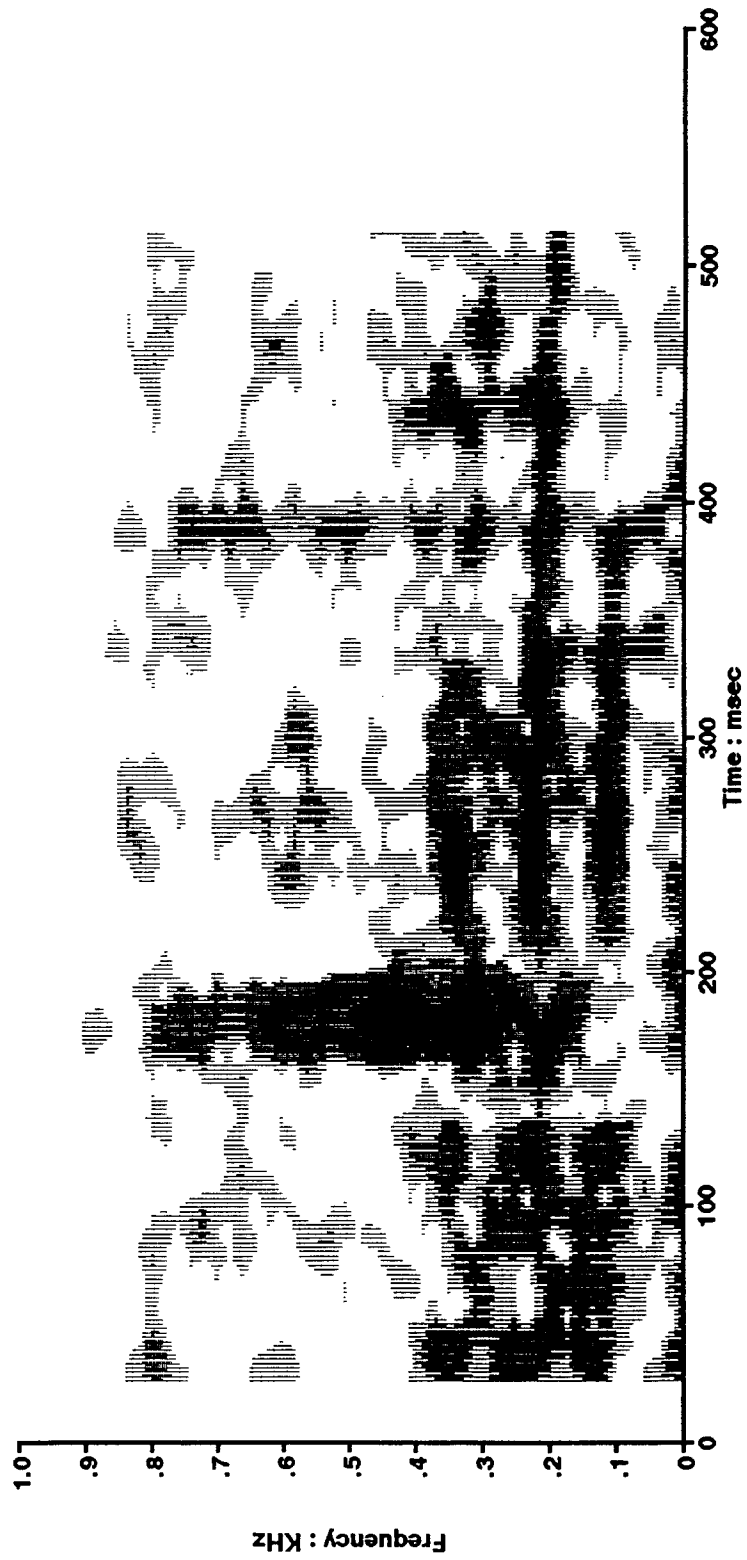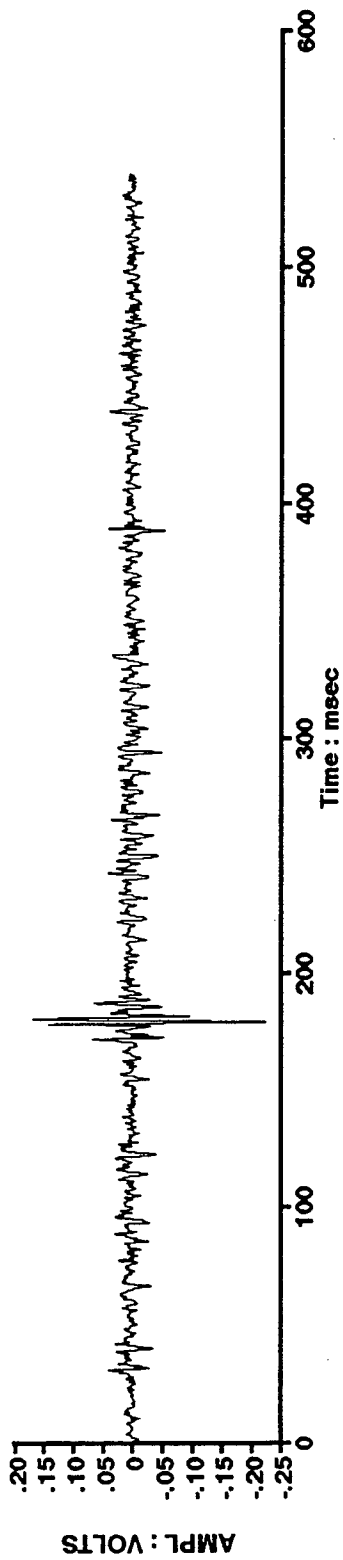
Figure 11. Ratio of pulse durations of different pulses in the call produced during the signal jump. P-values are the result of paired t-tests of pulse durations (not ratios).
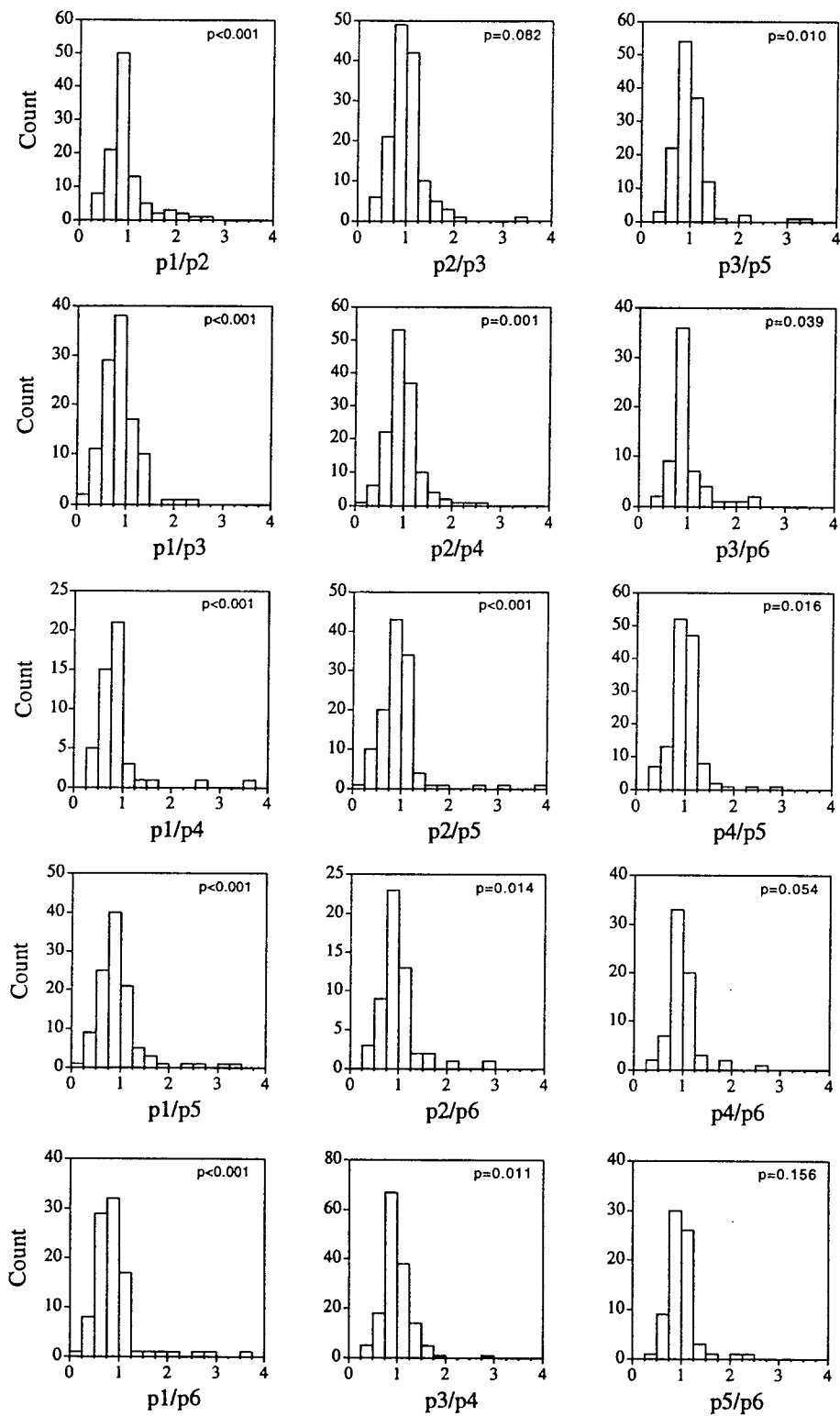
Figure 12. Linear regression of pulse duration and inter-pulse interval (IPI) on pulse

period for A. the signal jump, and B. aggressive sounds.

A.

$y = 0.660x + 26.602 \qquad r^2 = 0.645 \quad \square \quad$ IPI

$y = -0.137x + 53.859 \qquad r^2 = 0.006 \quad \triangle \quad$ Duration
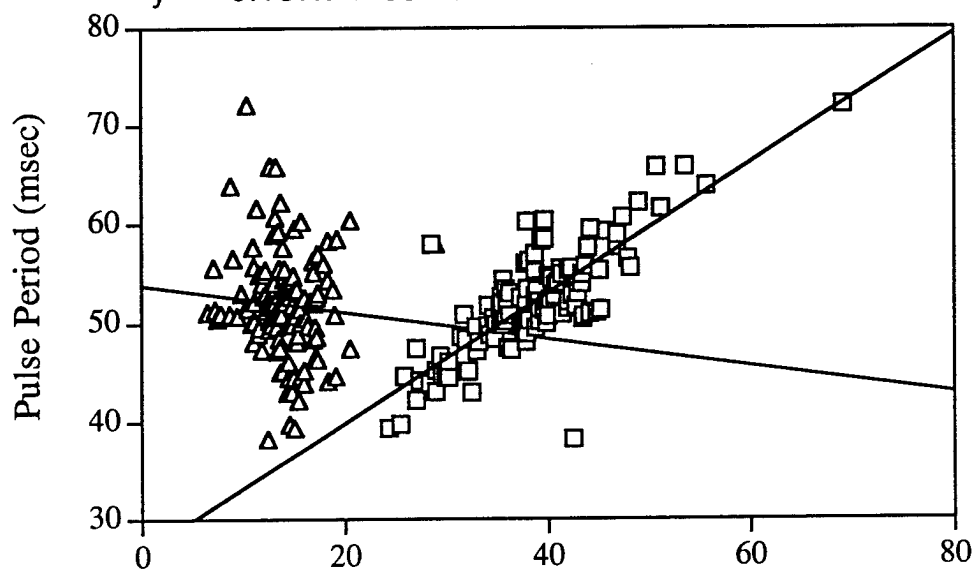
B.

$y = 0.976x + 16.086 \quad r^2 = 0.943 \qquad \square \quad$ IPI

$y = 0.607x + 39.347 \quad r^2 = 0.019 \qquad \triangle \quad$ Duration

IPI or Duration (msec)
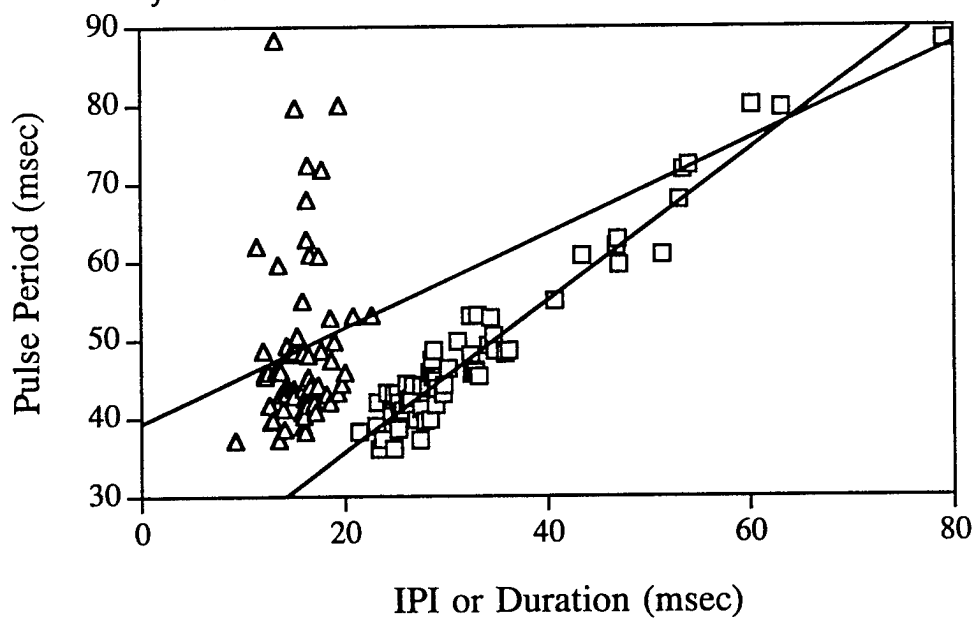
Figure 13. Call characteristics of the signal jump sound produced by *D. albisella* at Johnston Atoll and Hawaii (means (squares) and 1 standard deviation (error bars)).
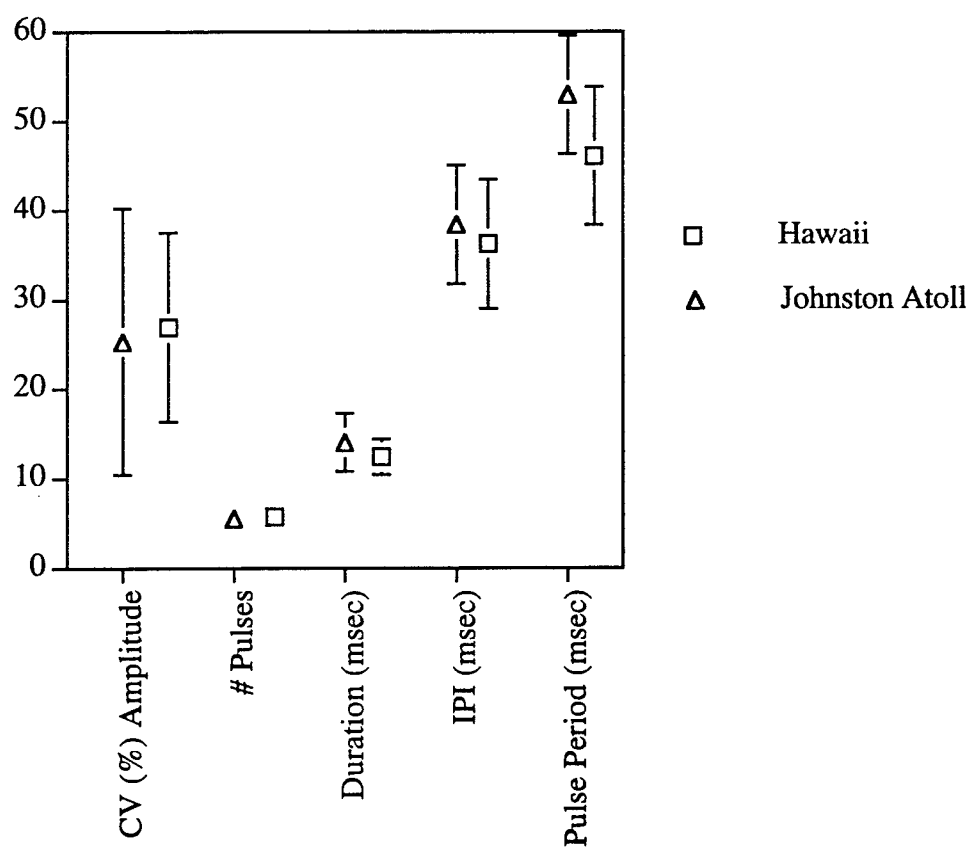
# Chapter III


# Courtship Sounds and the Acoustic Environment

# Abstract

The pulsed sounds produced during the signal jump of the damselfish <u>Dascyllus</u> <u>albisella</u> were analyzed to determine what information they contain about the signal jump and how they change with propagation. There was no relationship between signal jump speed or distance with the number of pulses or pulse period of the sound. There was no consistent change in the peak frequency of pulses in a call. If echoes were present in the sound, the change in echo delay would likely have been too small for damselfish to detect. Sounds attenuated with distance such that the signal to noise ratio decreased from 17-25 dB at 1-2 m to 5-10 dB at 11-12 m. It is unlikely that <u>D.</u> <u>albisella</u> can detect sounds at or beyond 11-12m from the sound source, based on noise masking data from other fishes. Pulse period is least affected by propagation when the percent of variation is compared to peak frequency, pulse duration, inter-pulse interval, and coefficient of variation of pulse amplitudes within a call. These results suggest that the sound produced during the signal jump acts over short distances and that the pulse period provides the most reliable basis for signal detection.

## Introduction

Many damselfishes (Pomacentridae) produce a pulsed sound during the courtship display known as the signal jump, in which a male rises in the water column and then swims rapidly down while making a sound. Because the male fish is swimming down while producing the sound, there might be information in the signal about how far and fast the fish are swimming that could be used by females in judging the quality of prospective mates who will guard their eggs for four to five days before hatching. The information in the sounds could be produced by physical limitations on the number of pulses in a signal jump of a given distance or by a correlation between the energy available for producing rapid pulsation and swimming speed. Information could also be provided by the acoustic environment of the fish, in which changes in the delay of echoes from the surface or changes in the peak frequency of consecutive pulses would be related to the depth of the fish at the time of sound production.

While the acoustic environment could provide information about the sound-producing fish, it could also limit the detectable range of the signal. The acoustic environment can greatly affect propagation of animal sounds in air, where wind, temperature gradients, the ground, and foliage can restrict or enhance the distance over which signals can be used for communication (Marten and Marler, 1977; Wiley and Richards, 1978; Richards and Wiley, 1980; Brenowitz, 1982; Wells and Schwartz, 1982). There has been little work on the effect of sound propagation in shallow water on sounds produced by fishes. Playbacks of the tonal boatwhistle of the toadfish (Opsanus tau) lost 18 dB over 5m in 1m water depth, restricting communication to several meters (Fine and Lenhardt, 1983). Grunt sounds produced by the squirrelfish Myripristis violaceus and Myripristis pralinius, were recorded in 5m depth water and attenuated 10 dB to about 25 dB signal to noise ratio (SNR) over 30 cm (Horch and Salmon, 1973).

There have been no studies on the propagation of the sounds produced by damselfishes. Based on the levels of background noise, the sound produced by the

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damselfish <u>Stegastes</u> <u>partitus</u> was expected to be detectable over distances of only 5m (Myrberg, 1980). It has been hypothesized that the temporal patterning of fish sounds is the most important factor for discrimination and sending information, and it has been shown to be important in species discrimination of pulsed sounds (Myrberg and Spires, 1980; Winn, 1964). However there have been no measurements of the effect of propagation on call characteristics of pulsed fish sounds.

This paper addresses the questions of what information is contained in the sound produced during the signal jump of the damselfish <u>Dascyllus</u> <u>albisella</u>, how far the signal can be detected, and how the characteristics of the sound vary with distance.

## Methods

## Recordings

Recordings of sound production were made while diving with a SONY V-9 video camera coupled to a hydrophone (flat response 10 Hz to 3000 Hz; with a nominal calibration of -162 dB re 1V/uPa), and with a SONY Professional Walkman with two hydrophones in April 1994. Floats were attached to the end of the hydrophones and the cables were taped to booms that were rested on the bottom, so that the hydrophone floated 0.5 m off the bottom. The hydrophones were placed so that the sound-producing fish were 1-2 m away.

## Video Analysis of Signal Jump

Video recordings of four males were made in 4m water depth. The fish were collected after they were recorded and their standard length was measured. The path of the signal jump was analyzed frame-by-frame (33 msec per frame) by marking the position of the fish eye on an acetate sheet. The position of a stationary object in the same plane as the

fish was also marked on the acetate to adjust for camera motion during the signal jump. Measurements of the standard length of the fish were also made from two or three different frames. The positions of the marks on the acetate were digitized, and the distance between marks was calculated based on the longest measurement of fish standard length. From these data the average signal jump swimming speed and distance were calculated.

The sounds produced during the signal jump were sampled at 10 kHz using the computer program SIGNAL (Engineering Design). The number of pulses and pulse period were calculated using the detection algorithm described in chapter 1, and regressed on the average signal jump swimming speed and signal jump distance.

## Analysis of Sound Propagation

Stereo recordings for propagation analyses were made in 7m water depth. The position of one hydrophone was fixed, while the other hydrophone was moved to the following distances relative to the fixed hydrophone: 0m, 1m, 2m, 4m, 8m, 10m. Recordings at "0 m" separation were made by placing the booms of the hydrophones next to each other, the hydrophones were separated by 2-4 cm. The recorded signals from both channels were sampled simultaneously at 25 kHz using SIGNAL, and low-pass filtered at 1000 Hz. The signals from the fixed and roving hydrophones were analyzed as above to detect the pulses and measure pulse duration, inter-pulse interval (IPI), pulse period, and coefficient of variation (CV) in amplitude of the pulses in a call. Analyses of pulse duration and IPI used pulses with SNR>19 dB. Cross-correlation analyses were performed on entire calls and pulses isolated from calls. The signal at the fixed (closer) hydrophone was used to determine the timing of the pulses, which were then isolated, including 4 msec before their on-times and 14 msec after their off-times.

Power spectra were calculated for each pulse in a call using an n-point FFT (where n was the number of points in the signal plus the number of zeroes padded to reach the next

highest power of 2) with a rectangular window. One-third octave band spectra were calculated from these power spectra. Attenuation was calculated at each of the distances between the fixed and roving hydrophones by averaging the 1/3-octave band spectra of all the pulses in a call and then averaging all of the calls. The differences in sensitivity of the hydrophones (evident in the 0m recordings) were not subtracted from the analyses. Attenuation was calculated as 20 log(roving hydrophone voltage/ fixed hydrophone voltage) for each 1/3-octave band. Noise level was measured using the captured signal up to 20 msec before the first pulse of the call and analyzed in 1/3-octave bands. The signal to noise ratio (SNR) of the roving hydrophone was calculated for each distance by averaging the SNRs of each pulse in a call and then averaging the SNRs of the calls. SNR was calculated as 20 log(signal voltage/noise voltage) for each 1/3-octave band.

## Results

### Distribution of <u>Dascyllus albisella</u> at Johnston Atoll

Most <u>D. albisella</u> were found in the lagoon of Johnston Atoll, where depths are typically 3 to 5 m, except in dredged areas where depths are 7 to 15 m. They were less abundant on the outer reef slope, where their range extended to depths of 30 m. They were rarely found near the reef edge. The shallowest <u>D. albisella</u> were in 1.2 m water depth. While all recordings were made with no intervening coral heads between the sound-producing fish and the hydrophone, there are many habitats where corals provide a natural obstruction to sound. In one area where 2-4 m wide coral pinnacles rise from 6m depth, <u>D. albisella</u> are located all around the coral heads and it would be impossible to make recordings 10 m away without an intervening coral head.

## Signal Jump Analysis

The signal jump was characterized by rapid, large beatings of the caudal fin followed by large displacements downward. Figure 1 shows a sample tracing of a signal jump and the frame-by-frame swimming speed. The signal jump swimming distance and speed were measured from the first large displacement to when the fish turned or the large displacements ended. The signal jumps averaged 0.8 mm/msec, with fish producing sound during 57.7% of the jump (Table 1). If there was an echo from the surface during a signal jump from 1 m above the bottom, the average increase in the echo delay from the first to the last pulse (assuming the fish were directly above the hydrophone) would be 0.25 msec (Table 1). The change in echo delay would be less if the fish were not directly above the hydrophone. In deeper water the percent change in the echo delay would be less (Table 1).

The number of pulses in a call and the pulse period were not related to either the signal jump speed or signal jump length (Fig. 2). The best relationship was between the number of pulses in a call and signal jump speed, but the variation in pulses only accounted for 15.4% of the variation.

The peak frequency of consecutive pulses in a call were analyzed to determine if the change in depth between pulses in a call produced consistent changes in their peak frequency (Fig. 3). There was no consistent relationship between pulse number and peak frequency. Similarly, the peak frequency of sounds made during the signal jump were compared to those made during visiting and mating for five males; signal jumps are made higher in the water column than visiting and mating sounds which occur on the bottom (see Chapter 2). There was no difference in frequency between sounds made during courtship and mating (Fig. 4).

## Sound Propagation

The effect of distance on sounds (including both courtship and aggressive sounds) was determined by comparing sounds received at two hydrophones separated by 0m, 1m,

2m, 4m, 8m, and 10m. Signals were evident up to hydrophone separations of 10 m (Fig. 5). Travel time between hydrophones was estimated by cross-correlating the signals from the fixed and roving hydrophones using both whole calls and pulses isolated from calls (Figs. 6 and 7). The sound speed was close to the predicted sound speed up to 4m, while it varied more at 8m and 10m. The correlations between the signals at the two hydrophones decreased with distance (Figs. 6 and 7).

To determine the effect of distance on call characteristics, the differences between each signal at the fixed and roving hydrophone were measured. The average peak frequency did not change much with distance, but the variance increased (Fig. 8). Pulse duration increased and IPI and CV of pulse amplitude decreased with distance, with most of the change in the first two meters (Fig. 8). Mean pulse period was least affected by distance. There are no data at hydrophone separations of 10 m for pulse duration and IPI, because they did not have a SNR>19 dB. There are also few data for pulse period and CV amplitude at 10 m because many pulses were not detected at the roving hydrophone that were detected at the fixed hydrophone using the signal processing algorithm.

Signals were most energetic between the 251 Hz and 501 Hz 1/3-octave bands (Fig. 9). The SNR in these bands decreased from 17-25 dB at 0 m hydrophone separation (1-2 m to source) to 5-10 dB at 10 m separation (11-12 m to source) (Fig. 10). Attenuation did not vary regularly with frequency band, but generally decreased with distance (Figs. 9 and 10). Of the most energetic frequency bands, the lower frequency bands (251 Hz and 316 Hz) attenuated up to 10 m, while the higher frequency bands (398 Hz and 501 Hz), attenuated most in the first 4m, with little attenuation afterward.

## Discussion

### Signal Jump

The sound produced during the signal jump did not contain information that could be used to predict the speed or distance travelled by the displaying fish. The factors that would be determined by the behavior of the fish, pulse number and pulse period, were not correlated with the swimming behavior of the fish. The peak frequency of the sound could be affected both by the behavior of the fish and by the environment. The resonance frequency of the swimbladder might be expected to increase as it decreased in volume during the dip. Yet the distance traveled by a fish while producing the sound (20 cm on average) would yield only a small change in swimbladder volume (1.5 % for a 20 cm dip starting at 3m depth). The variation in frequency between pulses might be the result of propagation effects, or due to changes in the tension on the swimbladder produced by the swimming fish.

At the highest calling rates there should be a relationship between calling rate and signal jump speed and/or signal jump distance. The highest calling rates that have been recorded are 80 signal jumps per minute (1 jump every 750 msec) (DM unpublished). The average signal jump time for this study was 451 msec. To make one signal jump every 750 msec would require faster or shorter swimming than this average signal jump (because the fish has to swim back up for the next signal jump).

### Echoes

There is equivocal evidence of echoes in the fish calls from several experiments. First, the duration of pulses in a call tended to increase with each pulse in a call (Chapter I). Part of this could be due to an echo from the surface, which would be delayed more and more as the fish swam down. The echo delay would change 0.25 msec from the first to the last pulse for the average distance swam during sound production (Table 1). Second,

propagation at distances greater than 4m showed little attenuation in the 398 Hz and 500 Hz

frequency bands. This could be due to an echo from the bottom. Since the hydrophones

are 0.5 m off the bottom and fish usually call 1-3 m from the bottom, the angle of incidence

is small at distances greater than 4m. Depending on the sound speed of the bottom, below

a critical angle there will be no transmission loss into the bottom (Rogers and Cox, 1988).

With such a short travel difference between the paths of the bottom reflection and the

straight path, the echo would not attenuate much compared to the direct path. Figure 11

shows the angle of incidence for a sound produced by a fish calling 1 m off the bottom

with a receiving hydrophone 1 m off the bottom. The critical angle for a fine sand bottom

is 28 degrees (for a bottom sound speed of 1700 m/sec). Third, the change in peak

frequency of pulses with distance, even at 1m, could be due to changes in the travel times

of echoes.

While there was some evidence of echoes other data contradicted the presence of

surface echoes. The duration of pulses increased from 1 to 4 m away from the fixed

hydrophone. As the distance from the source to the receiver increases, the echo delay

should decrease (Fig. 12). Furthermore, echoes could not be consistently confirmed in

analyses of individual pulses through autocorrelations and spectral analyses.

Autocorrelations should show a negative correlation at the echo delay, which should also

appear as a null in the power spectra at 1/echo delay.

Assuming that there was an echo, the change in echo delay would have been about

6.5% from the first to the last pulse in 4m water depth, and 3.2% in 7m water depth (Table

1). Goldfish (Carassius auratus) can detect 6% changes in echo delay when the echo is the

same intensity as the original signal, but only 20% changes when the echo is attenuated 15

dB relative to the original signal (Fay et al., 1983). If the detection abilities of damselfishes

are the same as goldfish, then the differences in echo delay from the first to the last pulse

would be undetectable or barely detectable. One final point concerning the detection of

changes in echo delays: if changes in delays are easier to detect at lower levels of echo

attenuation, then these should occur far from the source, where the path of the echo is not much longer than the direct path. However, there will be less change in echo delay farther from the source. Thus, there may be a narrow window over which echoes are detectable by fish in these environments, which will be affected by the depth of the water, the depth of the source, and the depth of the receiver.

## Propagation

Sounds could be detected up to 10 m from the fixed hydrophone. The pulse period of the call was less affected by distance than peak frequency, CV of amplitude, IPI, and pulse duration. This supports the prediction of Myrberg (1980), and suggests that pulse period may encode most of the useful information about a fish sound. Although, the number of pulses detected by the signal processing decreased with distance, it is not known how well fish would detect the number of pulses.

Auditory tuning curves of fishes have shown that they can be greatly influenced by ambient noise. In general SNRs are 15-20dB at thresholds of detection of pure tones in white noise (Buerkle, 1969; Chapman, 1973; Chapman and Sand, 1974; Fay, 1974; Hawkins and Sand, 1977; Fay, 1988). When there are directional differences between the noise sources and the sound source, the SNR at threshold decreases to 10-15dB (Chapman, 1973). The only data on masking in damselfish is from Stegastes partitus where the detection threshold is at 14 dB SNR (Ha, 1973). At 11-12 m (hydrophone separations of 10m) the SNR of D. albisella sounds was 11 dB. If their ability to detect sounds in noise is the same as other fishes, then it is unlikely that they could detect sounds at or beyond 11-12m from the source. However, the masking experiments were performed with tones, not pulsed sounds like those produced by damselfishes. They may be able to better detect pulsed sounds than tonal sounds as in the piranha, which can integrate temporal acoustic signals (Stabentheiner, 1988).

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D. albisella could possibly use the SNR and duration of pulses in a call to determine the range to the source. However, since these sounds are likely detectable less than 11-12m from the source, they could easily see the sound producer performing the signal jump.

The lack of attenuation in the higher frequency bands beyond 4m possibly as the result of bottom echoes was discussed above. However, the two lower frequency bands continued to attenuate beyond 4m. This might be due to the cutoff frequency of the channel, below which frequencies do not propagate. In a 7m channel the cutoff frequency ranges from 116 Hz (for a fine sand bottom) to 1070 Hz (for a sand-silt-clay bottom (Rogers and Cox, 1988). The bottom where the recordings were made was a complex mixture of ground coral, live coral, and coral rubble.

The propagation of sound in shallow water (shallow relative to the wavelength of the sound) is complex. There can be drastic changes in propagation depending on the depth of the sound source and receiver (Forrest et al., 1993). The complexities of the propagation can be seen in the variation in pulse durations over short distances. Even at 2-4 cm of separation between hydrophones, there is a lot of variability in the duration of pulses received at each hydrophone (Fig. 8). At hydrophone separations of 10 m, one of the pulses of the signal in figure 5 was much less attenuated than the others.

This study utilized two hydrophones at one depth to gain an understanding of what parameters of the sounds produced by D. albisella are unaffected by distance, and the distance over which the signal is likely detectable. While hydrophone arrays and known sound sources would be necessary to fully characterize the propagation of these sounds, the results support predictions that damselfish sounds are used over short distances, and that the most faithfully propagating information is contained in the pulse period of the sound.

The diversity of acoustic habitats in which D. albisella are found, from 30 m depth on a sloping bottom, to 1.2 m depth on a flat bottom, should select for signals that will be useful a wide variety of situations. It is unlikely that echoes play a major role in the

courtship behavior of <u>D. albisella</u> based on their detectability, but it is also unlikely that they would be crucial since they would be virtually absent in some habitats (like 30 m depth). Sounds used over short distances with information encoded in pulse period should provide robust communication in a wide variety of acoustic environments.

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Table 1. Signal jump statistics and the potential effect of movement during sound production on echoes.

|  | Mean | SD | Minimum | Maximum | n |
|---|---|---|---|---|---|
| Signal Jump Speed (mm/msec) | 0.8 | 0.2 | 0.5 | 1.2 | 15 |
| Signal Jump Distance (mm) | 339.3 | 104.3 | 138.0 | 564.0 | 15 |
| Distance swam while making sound (mm) | 193.4 | 76.7 | 112.4 | 347.7 | 15 |
| Percent of jump making sound | 57.7 | 16.1 | 41.1 | 88.0 | 15 |
| Maximum change in distance echo travel (mm) | 387 |  | 225 | 696 |  |
| Maximum change in time of echo delay (msec) | 0.25 |  | 0.15 | 0.45 |  |
| Echo Delay in 4m depth (msec) | 3.9 |  | 3.9 | 3.9 |  |
| Echo Delay in 7m depth (msec) | 7.8 |  | 7.8 | 7.8 |  |
| Percent change in 4m depth | 6.5 |  | 3.7 | 11.6 |  |
| Percent change in 7m depth | 3.2 |  | 1.9 | 5.8 |  |

Figure 1. Frame-by-frame position of a male *D. albisella* during a signal jump. Each point represents the position as traced onto acetate for a single frame. Each frame was separated by 33 msec. Start and End indicate the starting and ending points of the signal jump. The lower graph shows the swimming speed for each frame of the signal jump.
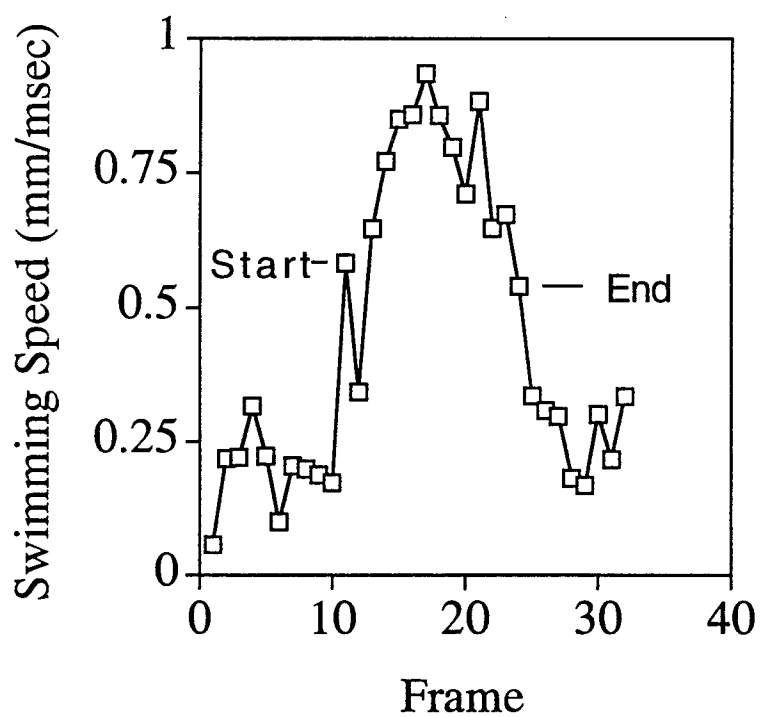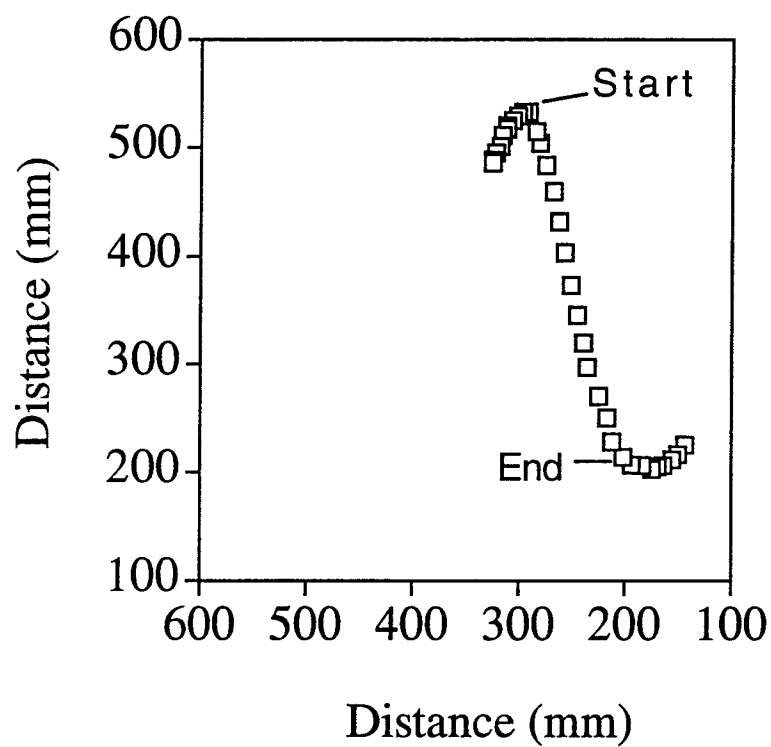
Figure 2. A. Regression of pulses on signal jump speed (squares) and signal jump length (triangles; second y-axis). B. Regression of pulse period on signal jump speed and signal jump length.

**A.**

y = 0.129x - 0.031      $r^2$ = 0.154   □     Signal Jump Speed (mm/msec)

y = 34.100x + 132.424   $r^2$ = 0.053   ▲     Signal Jump Length (mm)

**B.**

y =  -0.002x + 0.864    $r^2$ = 0.002   □     Signal Jump Speed (mm/msec)

y = 0.700x + 303.416    $r^2$ = 0.001   ▲     Signal Jump Length (mm)
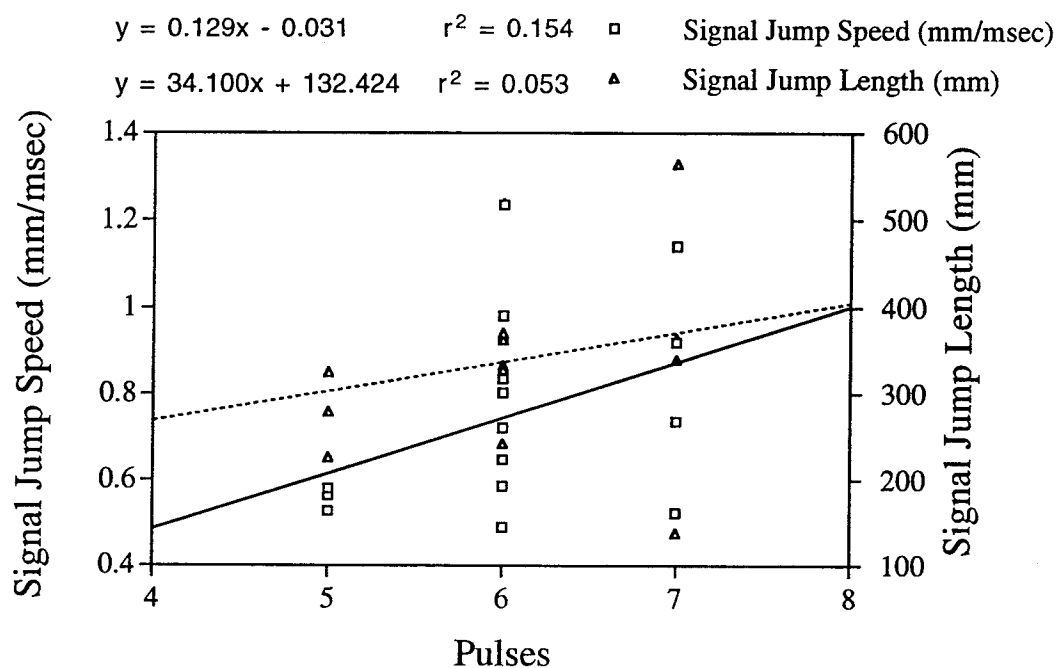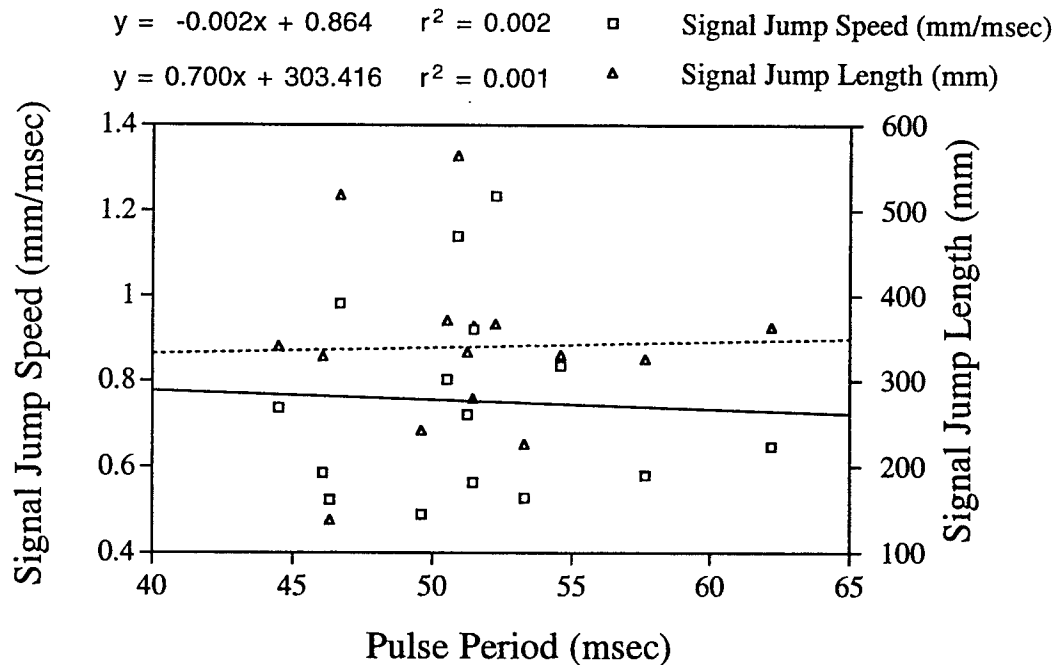
Figure 3. Frequency of pulses in a call for sounds analyzed in the signal jump analysis. Lines are drawn to aid in identification of pulses belonging to the same call.
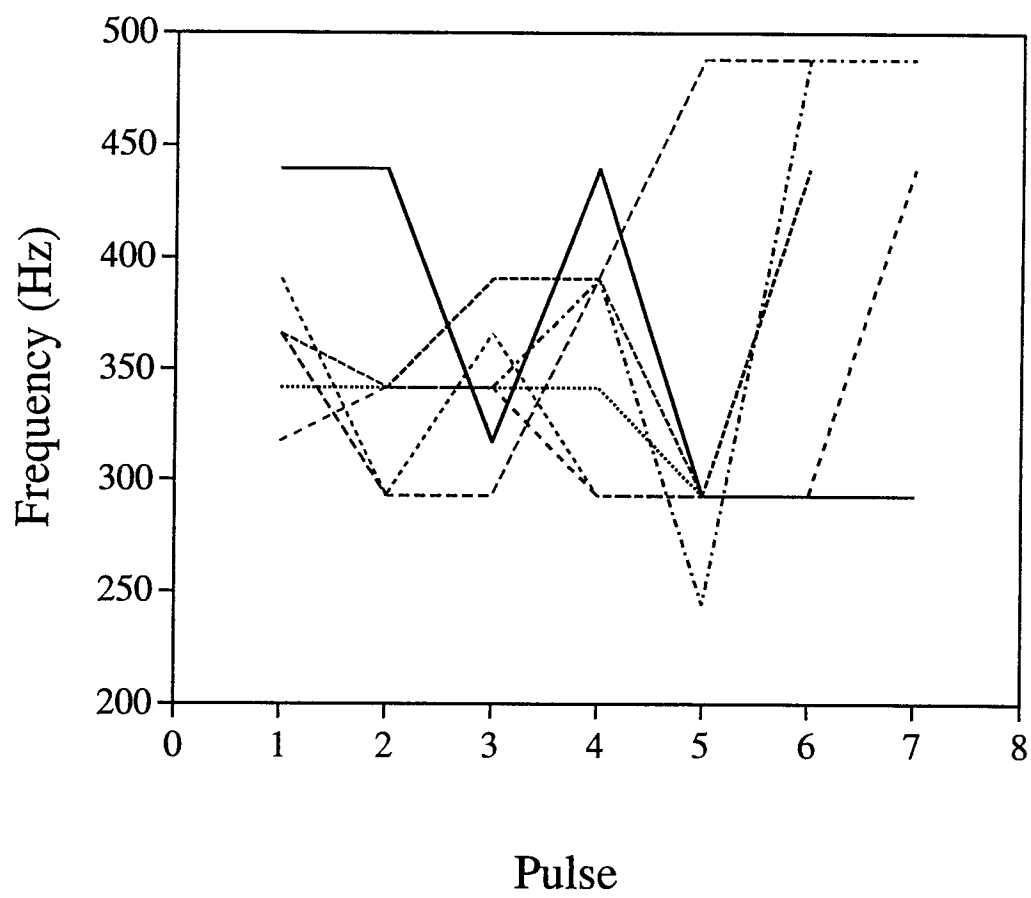
Figure 4. Peak frequency of courtship (squares) and mating (triangle) sounds produced by five fish (mean and 1 standard deviation).
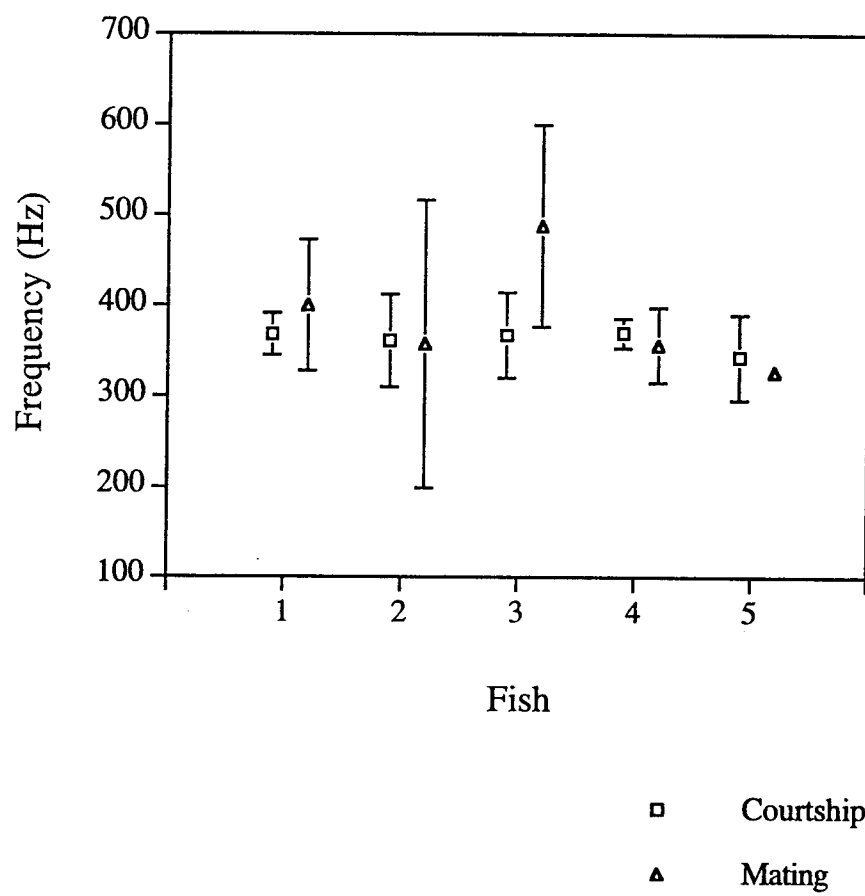
Figure 5. Oscillograms of the calls from the fixed and roving hydrophones. The distances indicate the separation between the fixed and roving hydrophones. Each pair of signals is a separate call.

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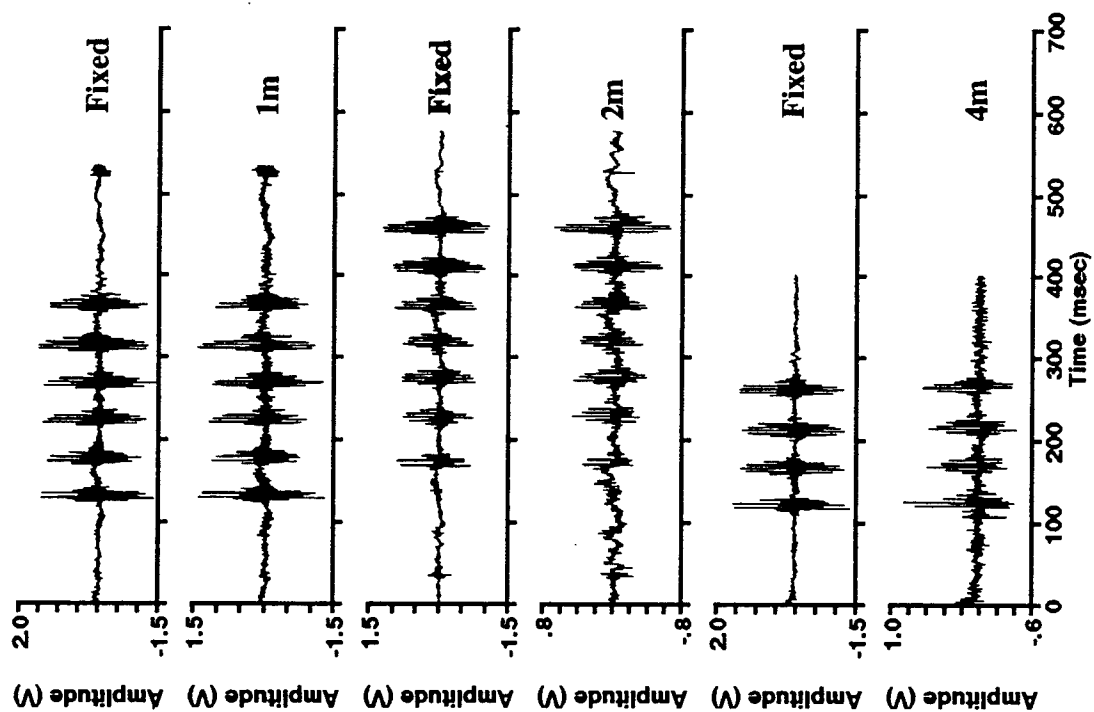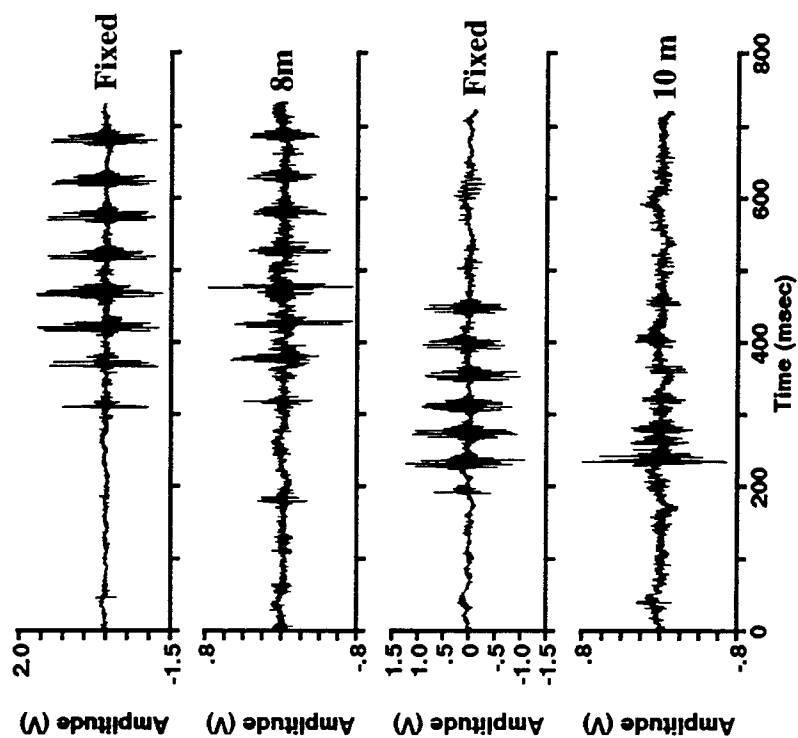
Figure 6. Travel time between the fixed and roving hydrophones (call dt) by the amount of

hydrophone separation. Travel times are the lags from a cross-correlation of the signals

received at the fixed and roving hydrophones that produced the maximum positive

correlation. The correlations (call r) for these lags are shown below.

$$y = 0.804x - 0.240 \quad r^2 = 0.799$$
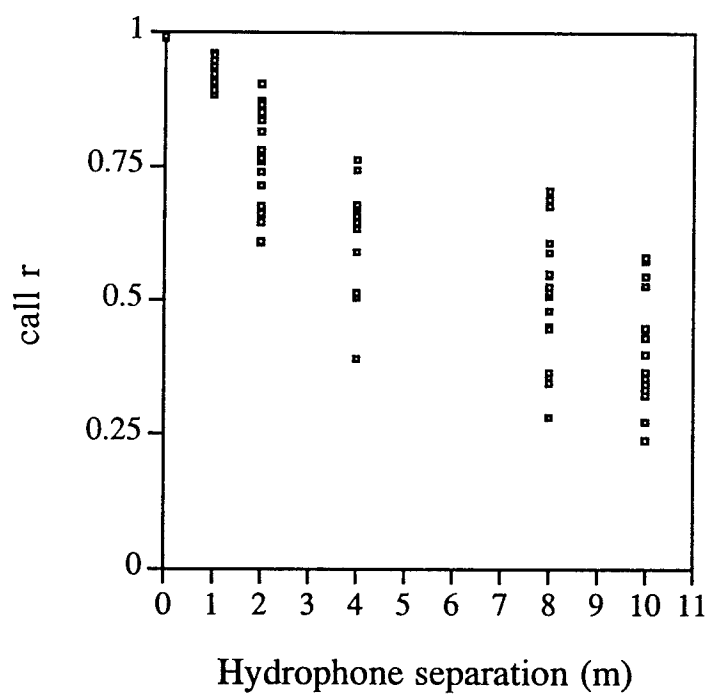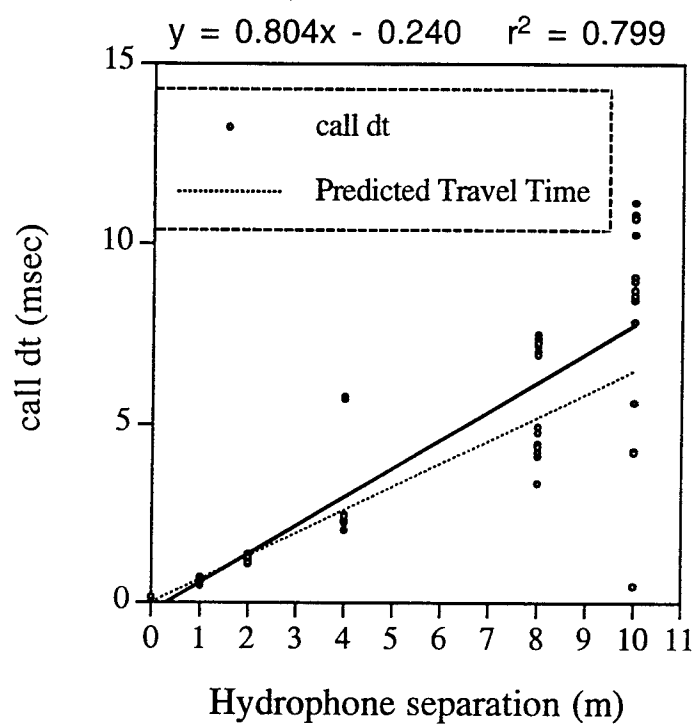
Figure 7. Same as figure 6, but each point represents the average lag (top graph) and correlation (bottom graph) of the cross-correlation of individual pulses from a call.

$$y = 0.805x - 0.199 \quad r^2 = 0.720$$
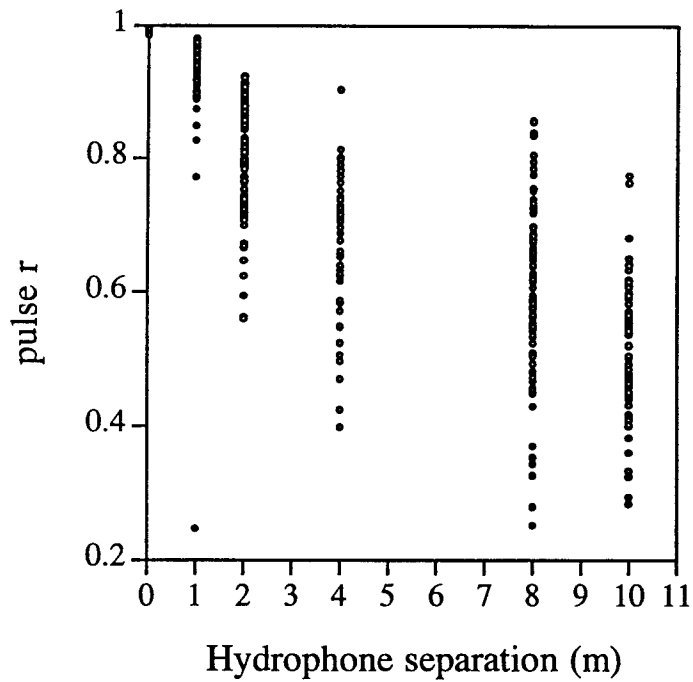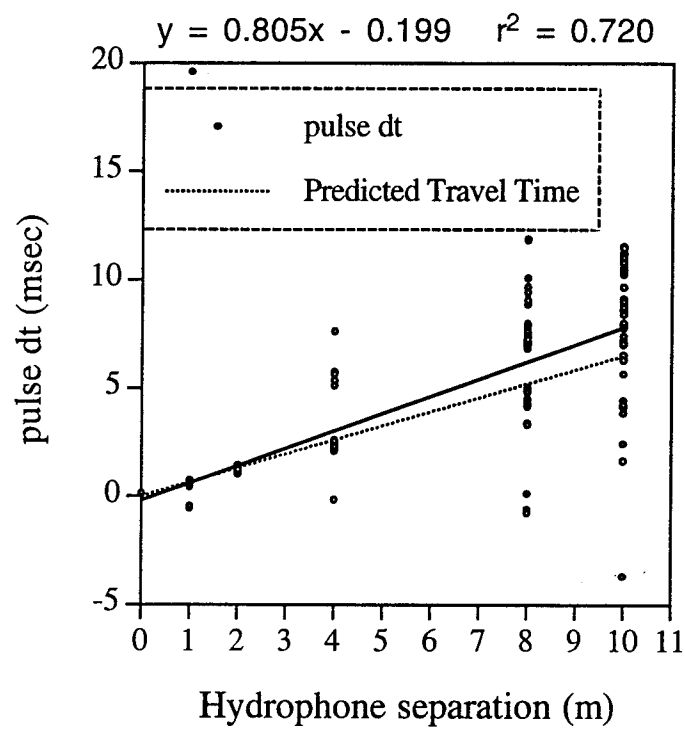
Figure 8. Difference in call characteristics at the fixed hydrophone minus the roving

hydrophone by the amount of separation (mean and 1 standard deviation (1st y-axis)). Call

characteristics are peak frequency, pulse period, CV of pulse amplitudes within a call,

pulse duration, and inter-pulse interval (IPI). The second y-axis is the percent deviation

from the average value of the parameter.
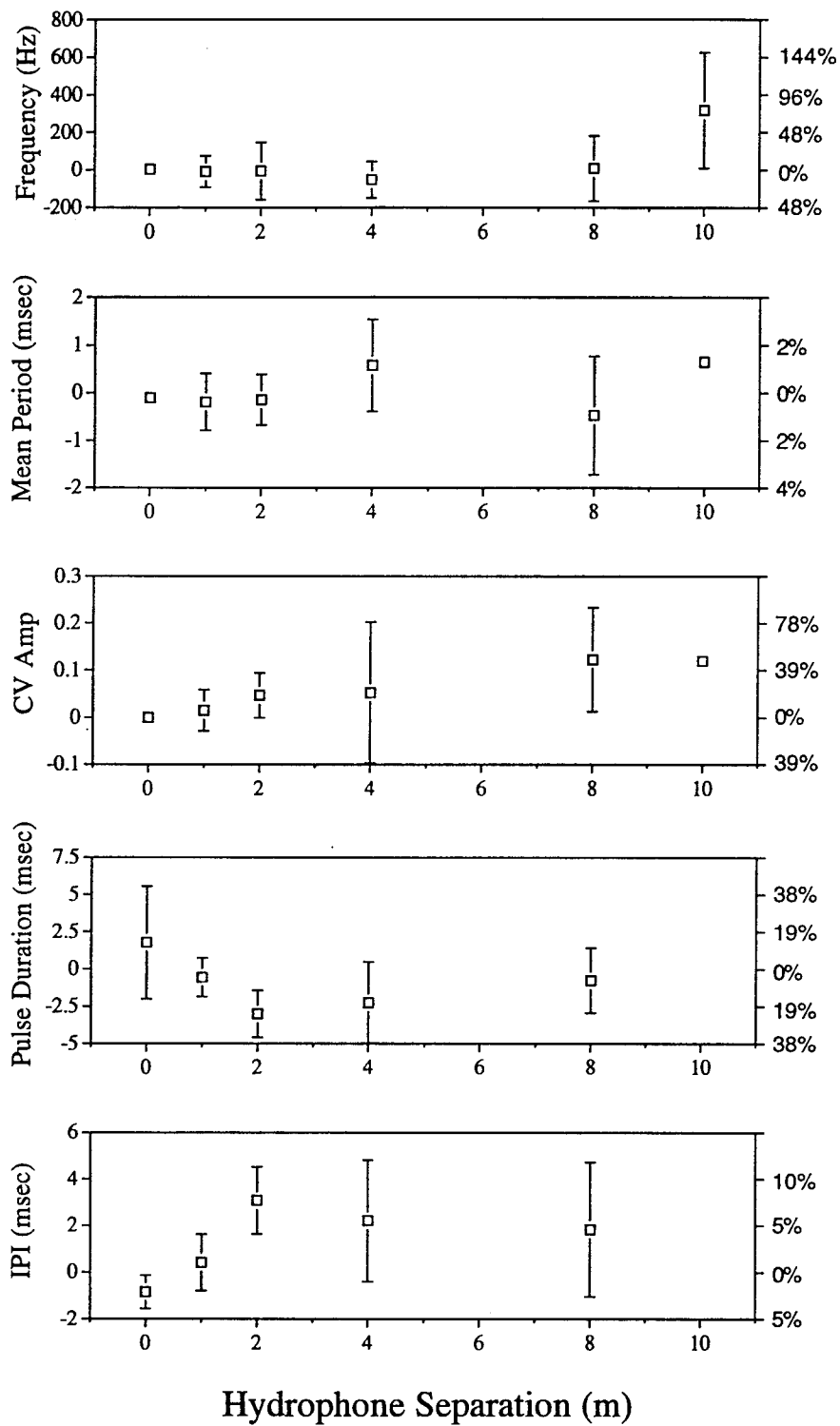
Figure 9. 1/3-octave band spectra of average A. attenuation, and B. SNR at the roving hydrophone.

A.
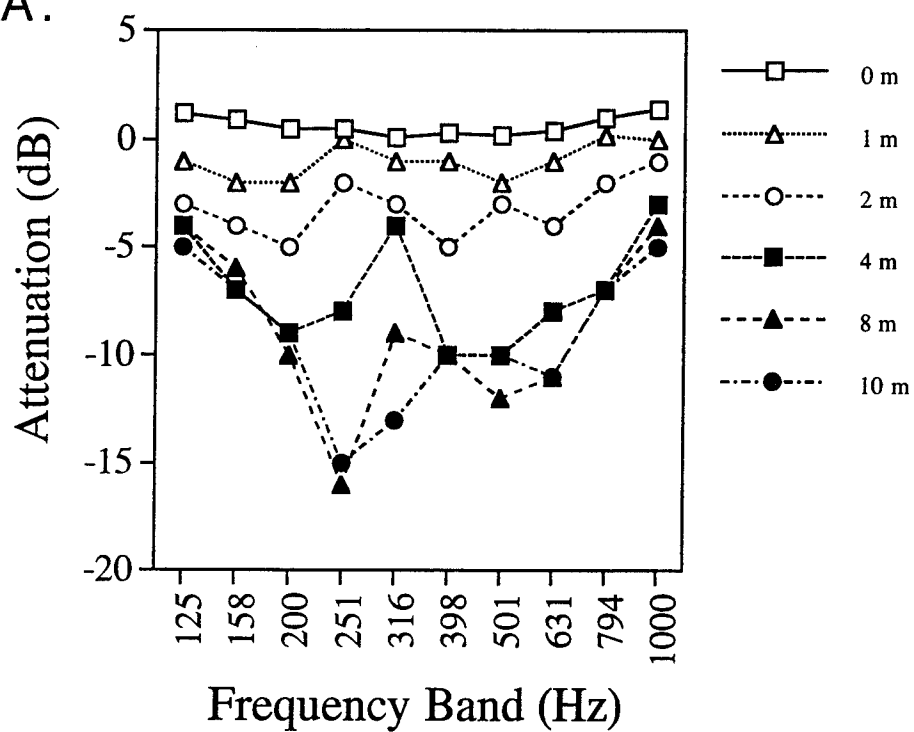
B.
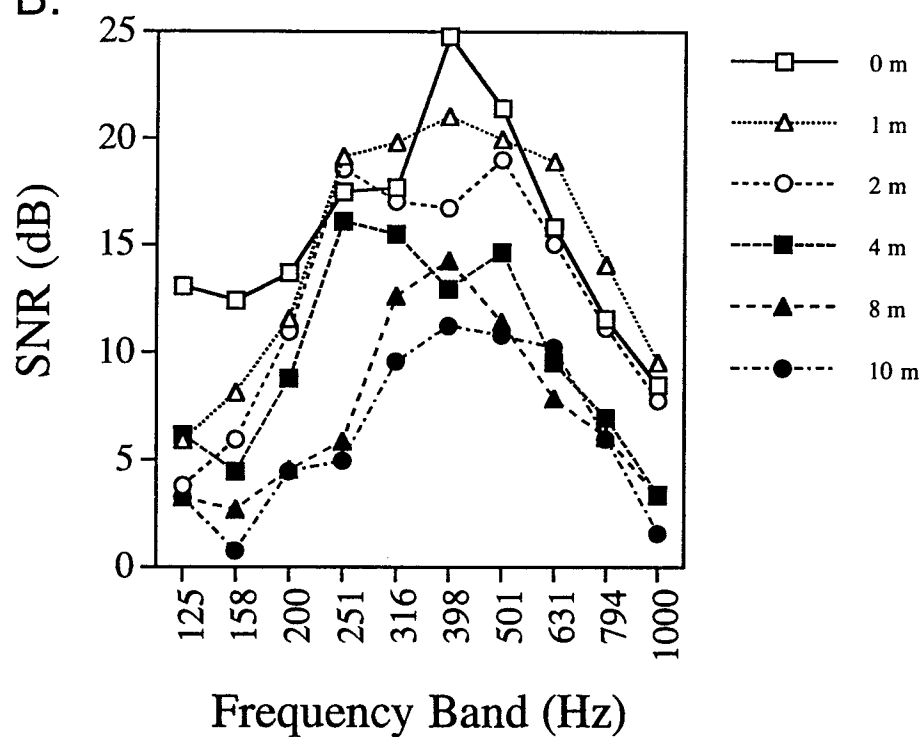
Figure 10. A. Attenuation with distance for the four most energetic 1/3-octave bands. B.

SNR of the signal at the roving hydrophone for the four most energetic 1/3-octave bands.

A.
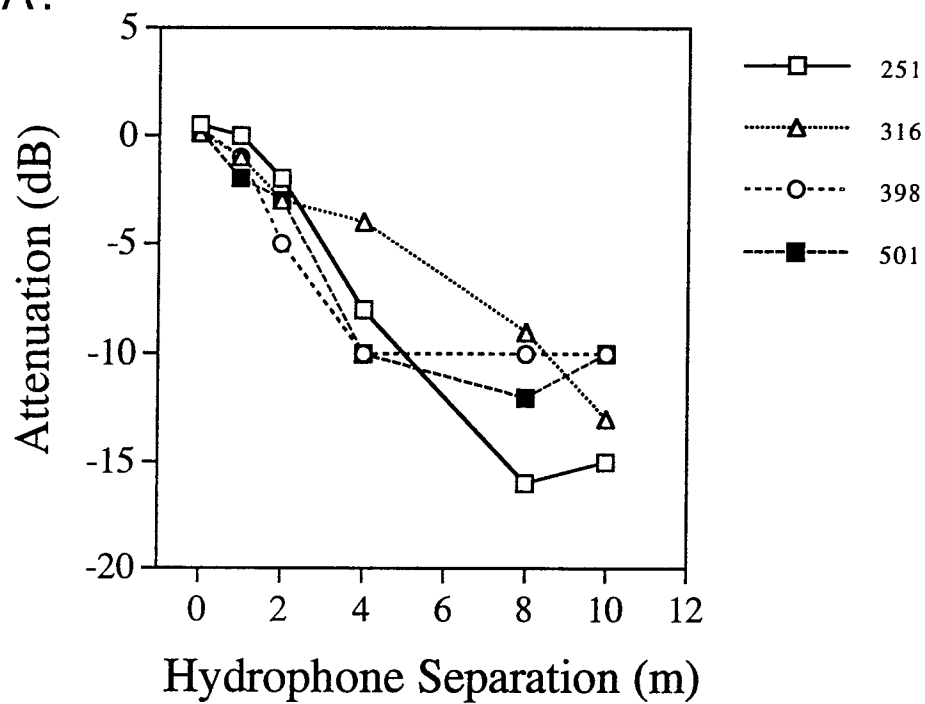
B.
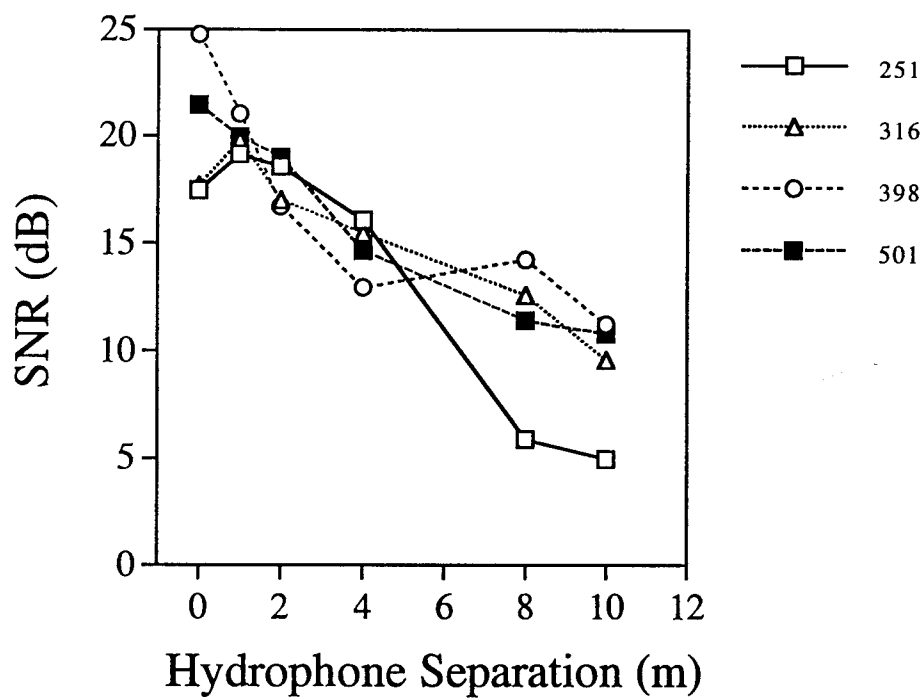
Figure 11. The angle of incidence for a sound produced by a fish calling 1m off the bottom

with the hydrophone 1m off the bottom in 7m water depth. The dotted line indicates the

critical angle for a fine sediment bottom (sound speed 1700 m/sec).
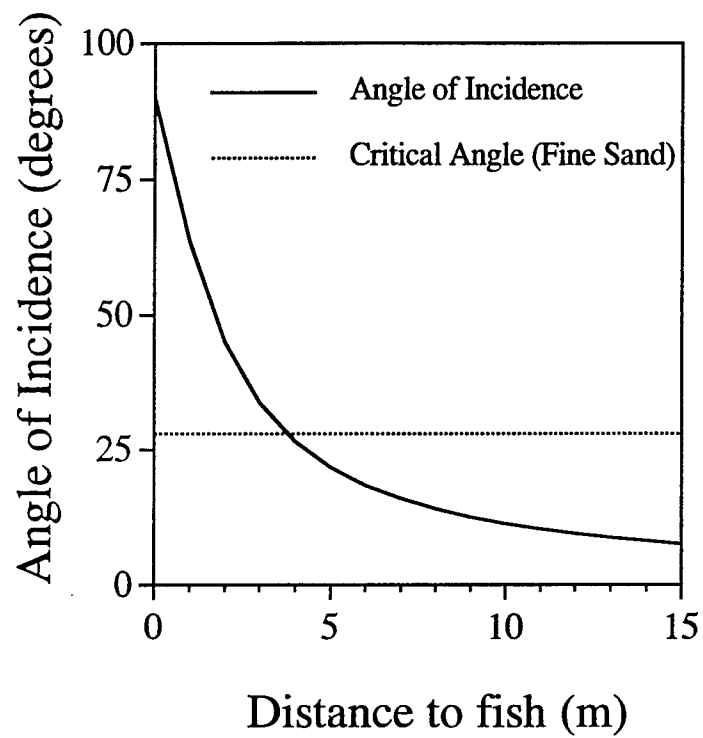
Figure 12. Predicted surface echo delays as a function of the separation between the sound source and receiver for a signal jump produced 1m from the bottom in 4m (dotted) and 7m (solid) water depth with the hydrophone 1m off the bottom.
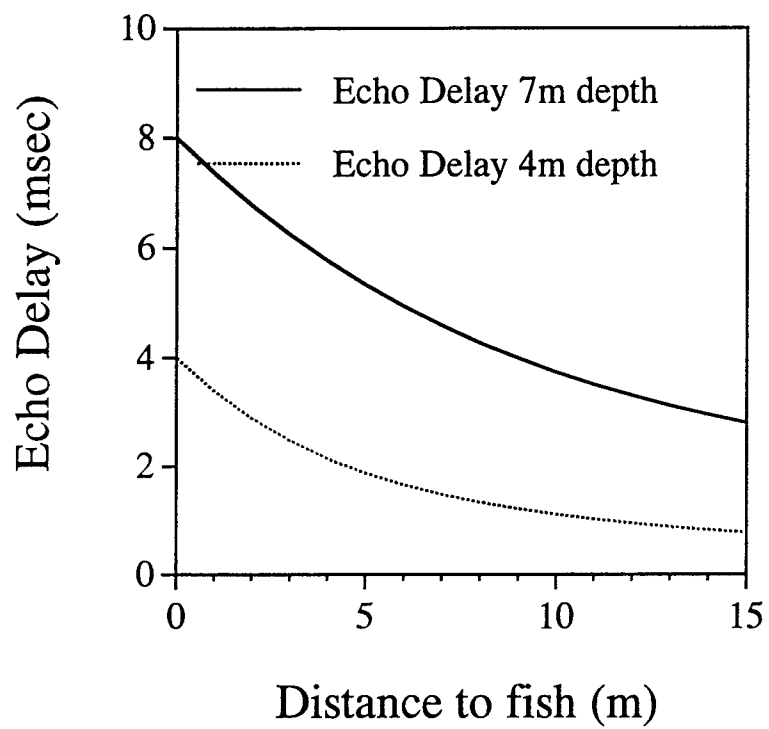
# Chapter IV

# Passive Acoustic Detection of Sounds Produced by the Damselfish, *Dascyllus albisella* (Pomacentridae)

# ABSTRACT

We developed and field-tested a passive acoustic detector that collects data on sound production by sonic fish. The detector was deployed to measure the timing of sound production by males of the damselfish, <u>Dascyllus</u> <u>albisella</u> (Pomacentridae), at Johnston Atoll, Central Pacific Ocean. Sound production rates were higher during the reproductive season (April) than during the non-reproductive season (October). The highest rates of sound production occurred on the day before and day of egg-laying. Sound production rates decreased during brood care, and increased again after hatching. The correlation of sound-production rate with the spawning cycle provided a reliable acoustic signal that was monitored by the detector. This new technology provides a capability for obtaining detailed measurements of reproductive activity over long time periods. Multiple detectors can be used simultaneously to monitor reproduction over large spatial scales.

# INTRODUCTION

We invented and tested a new oceanographic instrument that monitors fish reproductive activity using passive acoustic detection of courtship and mating sounds. This detector monitors individuals within a delineated area, and multiple detectors can be used to monitor populations over wide spatial scales. Most importantly, this device provides continuous time-series measurement of reproduction that can be matched to data recorded by physical oceanographic instruments simultaneously.

Quantitative measurement of reproductive cycles is crucial to an understanding of the population biology of fishes. In comparison with many other reef fishes that spawn planktonic eggs, reproduction in pomacentrids is more easily studied because they lay demersal eggs. However, measuring reproduction simultaneously at many sites over large spatial scales (e.g. tens to hundreds of kilometers) on a daily basis is not logistically feasible.

Earlier studies on the timing of sound production and reproduction suggest the potential broad applicability of using passive acoustic detection technology with sonic fishes. Johnson (1948) first suggested the diurnal and seasonal occurrences of fish sounds might be useful to study the ecology of fishes. Brawn (1961) found that the level of sound production and reproduction in the cod Gadus callarias (Gadidae) varied both seasonally (highest from September to November), and daily, with peaks of sound production after dusk associated with spawning. Lobel (1991) found that the parrotfish, Scarus iserti (Scaridae), produced a broad-band sound during the spawning rush, and that the hamletfish, Hypoplectrus spp. (Serranidae), produced specific sounds during courtship and mating. The time and place of spawning of several sciaenids, Pogonias cromis, Bairdella chrysoura, and Cynoscion nebulosus, have been identified using hydrophones and listening for sounds produced by spawning aggregations (Mok and Gilmore 1983, Saucier et al. 1992, Saucier and Baltz 1993).

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We tested the ability of the passive acoustic detector to quantify patterns of sound production and reproduction with the pomacentrid Dascyllus albisella. Pomacentrids are well-known sound producers (e.g. Myrberg 1972, Spanier 1979, Chen and Mok 1988). Male D. albisella are territorial and produce stereotypical sounds associated with courtship and mating, making them ideal for testing this detector (Lobel and Mann 1995). The purpose of this study was to evaluate the feasibility and utility of using sounds to quantify patterns of pomacentrid reproduction.

## MATERIALS AND METHODS

Passive Acoustic Detector

The passive acoustic detector consists of a sonobuoy (an FM-wideband radio transmitter on a surface buoy) connected to a hydrophone (BioAcoustics, Box 549, Woods Hole, MA) anchored in an individual male's territory. Sounds are transmitted from the hydrophone by the radio transmitter to a nearby laboratory where they are received and processed through a bandpass filter (between 200 Hz and 600 Hz) to reduce noise from other sound sources. The dominant energy in the calls produced by Dascyllus albisella is in this frequency range (Lobel and Mann 1995). The filtered sounds are then processed by our custom-built signal detector that recognizes individual sound pulses and measures and stores to computer pulse duration (ms), pulse amplitude, and the time of sound production (ms). The acoustic detector is capable of processing input from four separate sources simultaneously, sampling each of them at 1 kHz. Since we are not estimating the signal frequency, there is not a problem with aliasing.

The calls produced by D. albisella contained multiple pulses and were reconstructed from the computer data file using the following species-specific criteria, based on the pulse and call characteristics of courtship calls (Lobel and Mann 1995):

1.   Accept pulses with duration > 5 msec and < 50 msec.

2.   Group pulses into a call if two consecutive pulses are within 30-79 msec of each other. Otherwise begin constructing a new call.

3.   Discard 1- and 2-pulse calls.

The resulting data set includes: the time of a call (ms), number of pulses, call duration (ms), and the amplitude of the call. Calling rates were calculated by binning the data into time periods of 10 minutes, 1 hour, and 1 day.

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## Field Study

The acoustic detector was deployed at Johnston Atoll, Central Pacific Ocean, (16° 44.2' N, 169° 31.0' W) in October 1993 and April 1994. Data on sound production activity was collected for one male (male 2) D. albisella in October 1993 when no reproduction took place, and for three males in April 1994, all of which spawned during the study period. In April, two individuals were monitored simultaneously. One hydrophone was located in the territory of male 2 from April 1-20. The other hydrophone was located in the territory of male 1 from April 1-15, and was then.moved to male 3 from April 16-28. The input volume was controlled using attenuators on the detector. The acoustic signal was monitored in the laboratory on audio speakers and LED lights on the detector indicated when a sound was detected on a given channel. The attenuator was adjusted so that the input levels to the channels were equal and D. albisella sounds were only detected on one channel at a time, so that the same sound was not detected simultaneously by two different channels. The input level was not changed when the hydrophone was moved from male 1 to male 3.

The nesting status of eight males was visually assessed daily from April 1-28, between 0800-1200h. In October surveys were made October 14, 16, 20, 22, and 27. Quantitative measurement of brood sizes was not possible due to their irregular shape, accessibility, and because they occurred on substrates with varying topography, from flat rocks to highly structured Acropora spp. coral. Brood sizes were estimated by comparison to a standard area of approximately 185 cm$^2$, and then were assigned to a size category. The approximate ranges of the brood-size categories are: brood size 0=no eggs, brood size 0.5=>0-139 cm$^2$, brood size 1=139-278 cm$^2$, brood size 2=278-463 cm$^2$, brood size 3=463-648 cm$^2$, brood size 4=648-833 cm$^2$, brood size 5=833-1018 cm$^2$. Male territories were mapped by measuring the distance and compass bearing between pairs of

sites. The distances between male territories are: male 1-2=11.1 m, male 2-3=8.0 m, male 3-4=2.7 m, male1-3=16.6 m.

Light level (solar irradiance) was recorded using an integrated measurement every 10 minutes with a pyranometer sensor sensitive to 400-1100 nm (i.e. sunlight) (LICOR Inc., Lincoln, Nebraska).

Statistical tests were performed with StatWorks (Cricket Software, Philadelphia, PA). Spearman rank correlations ($r_s$) were calculated, since log and square root transformations did not yield normally distributed data for call rates in 10-minute bins.

## Calibration

For analysis of call detection accuracy, the transmitted signal from the hydrophones was split with one input to the detector and the other input to a tape recorder (SONY Walkman Professional WM-D6C). These sounds were manually analyzed in the laboratory using the signal processing program SIGNAL (Engineering Design, Belmont, MA) and compared to the reconstructed calls recorded by the detector.

# RESULTS

## Accuracy of the Acoustic Detector

To measure acoustic detector accuracy, calls recorded on audio tapes were compared with the detected calls (Table 1). The purpose of the accuracy test was to determine: a.) if the device correctly detected calls by the single fish that was being monitored, b.) if calls of other, more distant Dascyllus albisella males were also detected,

and c.) if sounds from other fishes, such as squirrelfishes (Holocentridae), or other sources were detected and falsely categorized as D. albisella sounds.

D. albisella calls recorded on audio tapes were processed on a sound-analysis computer system, identified manually, and categorized based on amplitude as either proximate or background calls. Proximate calls were high amplitude D. albisella sounds, which were likely produced near the hydrophone by the resident male. Background calls had lower amplitudes and different frequency characteristics than proximate calls (Lobel and Mann 1995), and were likely produced by more distant males.

Accuracy tests of the detectors deployed in the territories of males 1 and 2 indicated that 96% of the calls were correctly detected (130 calls detected/136 calls), with less than 2% false detections of other individuals (3 false detects/151 calls). We could not determine whether the detector in the territory of male 3 was also detecting calls made by male 4, since his territory was nearby and not separately monitored. For male 3, 79% (328 calls detected/417 calls) of the proximate calls were detected, with 2% (11 false detects/458 calls) false detections of other individuals.

Sounds that might be falsely detected were grouped into those that were presumably produced by holocentrids (possibly Myripristis berndti), and those produced by other fishes (e.g. scarids and acanthurids) biting the hydrophone (Table 1). Sounds presumably made by holocentrids were produced at night (from 19:30 to 00:00), and none (0/46) of these were detected. 26.3% of the bites on the hydrophone produced false detections (5/19 bites), but they were rare relative to the number of correct call detections (5 hydrophone bites were detected out of a total of 458 D. albisella calls detected).

Sounds produced by SCUBA diver bubbles were also falsely detected (57 diver bubble calls detected/97 total calls detected). The acceptable pulse duration range was reduced (from 6-49 msec to 6-25 msec) to try to decrease the number of false detections, but this adjustment also decreased the number of correct call detections, so the range was left unchanged. The time periods when divers were present within 20 m of the hydrophone

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were recorded on each dive (mean±SD=20.75±14.3 minutes per day). Divers were in the study area for 21 minutes when the 57 false detections were made. The time periods of diver presence were not removed from the data.

## Calling Rate and Timing of Spawning

Reproduction in April was synchronized for the eight males within the study area, such that 72% (16/22) of the spawnings occurred on the same day, 23% (5/22) within one day, and 5% (1/22) within 2 days. Spawning was cyclic with 72% of the spawnings taking place on April 7, 13, 20, and 26. Brood care lasted four days for broods that were laid and hatched during this study (n=13 nests of 8 males). There were no overlapping broods. The beginning of spawning was never observed. Spawning was observed as late as 13:00, but was usually completed by 08:00.

The daily calling rates of males 1 and 3 increased prior to nesting with peaks either the day before or day of spawning, after which they rapidly decreased and remained low during brood care (Figure 1 a and b). After hatching, the calling rate of the males increased again. Thus, sound production regularly increased and decreased with the spawning cycle. The April 6 brood of male 1 did not develop, and embryos were not present on April 8. Calling at night peaked on the day of egg-laying (Figure 1 and 2).

Male 2 exhibited the same pattern of sound production as males 1 and 3, although embryos were not found in his territory on the first two laying cycles (Figure 1c). His calling rate decreased on each of these spawning cycles, even though he did not receive eggs. Since these sites were not surveyed until after spawning activity was completed, it is possible that spawning occurred and that the eggs were cannibalized or eaten by predators before the survey was conducted (07:40 on April 7; 11:00 on April 13). Male 2 received eggs on the third spawning cycle (April 20), and the pattern of sound production was the same as the patterns of other males.

The acoustic detector was deployed during October 1993 in the territory of male 2 (Figure 1d). We did not observe spawning by male 2 or any other male in October, although we did see visiting behavior by some females (n=3 observations of visiting behavior). A diel cycle in sound production occurred as in April. The calling rate in October was significantly lower than the calling rate during April (October: mean±SD 658±258, range=171-1064; April: 1205±631, range=499-2648; p=0.015, one-tailed t-test on log-transformed data) (Figure 1 c and d).

SCUBA bubble interference during this study was negligible, because divers were present for a short period each day (about 21 minutes) and the estimated number of false detections (about 57 per day) were low compared to the daily calling rates of the fish (daily calling rate range: male 1=623-3327, male 2=499-2648, male 3=1686-7850). The accuracy test for the detector indicated that the data from male 3 also included calling by another nearby fish, male 4 (background calls detected on main channel, Table 1). This contention is supported by data for the calling rate of male 3, which was more than twice as high as males 1 and 2 (daily calling rate mean±SD: male 1=1585±809, male 2=1205±631, male 3=4324±2493).

## Accuracy of Spawning Event Detection

Two features of sound production were associated with the spawning cycle in D. albisella. The highest daily rates of calling occurred on the day before and on the day of spawning, and calling rates between 0000-0600 peaked on the day of spawning. To quantify the accuracy of spawning detection the following paradigm was applied to the detector data. A day was designated as a spawning day if the total calls per day were at least twice the lowest levels three days before and three days after that date. If two dates

satisfying the previous criterion were within 2 days of each other, then the spawning day was designated as the day with the greatest number of calls from 0000-0600.

80% of the spawning events (4/5) were correctly designated; one spawning event was designated a day later than it actually occurred (April 25 spawning of Male 3). 4% (2/49) of the days were misclassified as spawning days, when no eggs were found (April 6 and 13 of Male 2). However, male 1 received eggs on both those days, and male 3 received eggs on April 13.

## Sound-Production Rate and Brood Size

To test the hypothesis that measures of calling rate could be used to estimate brood size, six measures of calling rate (maximum calls/10 minutes, calls/hour, and calls/day both the day before and after spawning) were correlated with brood size (n=6). The highest correlation was for maximum calls/10 minutes the day before spawning ($r_s$ =0.754, p=0.084). When fish 3 was excluded from the analysis, because it may represent calling by more than one male, the maximum calls/10 minutes was better correlated with brood size ($r_s$=0.949, p=0.051, n=4).

## Patterns of Sound Production

Most sound production took place during the daytime with lower levels of calling at nighttime (Fig 1 and 2). Sound production peaked each day at dawn (n=45 days sampled from 3 males) (Figure 2).

To test the hypothesis that calling rates were consistent over consecutive ten-minute time periods, the calling rate in one ten-minute period was plotted against the calling rate in the following ten-minute period (Male 1 $r_s$ =-0.170, p<0.001, Male 2 $r_s$ =0.313, p<0.001). Although these correlations are significantly different than zero, they are low. Most of the calling was less than 50 calls/ten minutes (Male 1 96% (2072/2153), Male 2 98%

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(2862/2916)). Periods with high rates of calling (>50 calls/ten minutes) were generally followed by periods with little calling (<50 calls/ten minutes) (e.g. % time periods with >50 calls/ten minutes followed by time period with <50 calls/ten minutes: Male 1 75% n=61/81, Male 2 81% n=44/54).

To test the hypothesis that adjacent males influence each others' calling rates, the calling rates (calls/10 minutes) of male 1 and male 2 were compared from April 1-15 ($r_s$ =-0.208, p<0.001). The correlation was significantly different than zero, but the correlation was low. Most calling (95%, n=2048/2153) was less than 50 calls/ten minutes, and high rates of calling (>50 calls/ten minutes) by one male were associated with low levels of calling by the other male (<50 calls/ten minutes) for 93% (n=98/105) of the data.

Periods with high rates of courtship probably result from female visiting events. One full visiting event in which one female traveled to the nests of three males was recorded on video and analyzed. The number of courtship calls in the time period preceding and during visiting are listed in Table 2. Calling rates of these three males increased 68-fold during female visiting. This was the only full visiting event recorded on video. Many visiting events were observed during the nest surveys, and the calling rates of the males were noted to be qualitatively much higher (n=25 events for 15 males in April 1994).

Since D. albisella are diurnal planktivores, one would suspect that they would be inactive at night (between sunset and sunrise). However, sound production was detected at night and was most intense just before spawning. We believe these sounds were calls by D. albisella and not from some other source because: a.) analysis of the audio recordings of the detector input showed D. albisella made sounds during the night (19:35 - 00:00) that were detected by the detector (Table 1), b.) divers heard sounds characteristic of D. albisella at night, and c.) the most likely potential source of non-D. albisella sounds, those produced by holocentrids, were not detected by the acoustic detector during calibration

tests. The sound-producing D. albisella were not seen during the night dives, so it is unknown whether they perform the signal jump with these sounds.

## DISCUSSION

Sound production by Dascyllus albisella peaked at dawn each day during the reproductive season and varied in intensity with the daily spawning cycle. Crepuscular peaks in sound production are common for sonic fishes. Steinberg et al. (1965) and Myrberg (1972) found dawn and dusk peaks in sound production by Pomacentrus partitus (Pomacentridae). Breder (1968) made observations on the timing of sound production of sonic fishes from 1961-1965, with virtually continuous year-round coverage. He found a peak in calling of the sea catfish, Galeichthys felis (Ariidae), at dusk, and that most boat-whistling of the toadfish, Opsanus beta (Batrachoididae), occurred at sunset. Winn et al. (1964) and Steinberg et al. (1965) found that sound production by the squirrelfish, Holocentrus rufus (Holocentridae), peaked at both dawn and dusk, with less during the day, and little at night. In contrast, Salmon (1967) did not find a crepuscular peak in the calling of the squirrelfish, Myripristis berndti (Holocentridae); most sonic activity occurred between 0500-1900h when they were aggregated in caves.

We have demonstrated that the passive acoustic detector accurately detects and records sounds made by D. albisella. The pattern of sound production was predictive of the timing of spawning on a daily basis for the fish studied. These results corroborate data from Dascyllus trimaculatus and Dascyllus marginatus, which also show increased courtship activity on days of spawning (Fricke 1973, Holzberg 1973). The lack of social facilitation of courtship by neighboring males (males 1 and 2) may be because a male courts

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most vigorously in response to female visiting, not other male courtship, and a female will not visit two males simultaneously, but is likely to visit several males during visiting.

False detections of spawning were rare. The two false detections of spawning occurred on days when immediately neighboring males received eggs. They did not occur during non-spawning periods. In this sense, the acoustic detector was accurately measuring female reproductive activity. Thus, one acoustic detector could be used to accurately monitor reproduction of a local group of D. albisella, even though the individual being monitored may not receive eggs during each identified spawning event.

The maximum calling rate (calls/10 minutes) on the day before spawning was positively correlated with brood size, and likely took place during female visiting, although the result was not statistically significant at $\alpha=0.05$. More males need to be sampled to statistically verify this relationship. These results corroborate those of Gronell (1989) who found that the calling rate during female visiting on the day before spawning in Chrysiptera cyanea (Pomacentridae) was correlated to male spawning success. Furthermore, signal jumping rates of Pomacentrus partitus were correlated to male reproductive success in two separate studies (Schmale 1981, Knapp and Warner 1991). These studies suggest that passive acoustic detection may be broadly applicable to measuring reproduction in pomacentrids. Co-mingling species may be more difficult to study, such as many of the pomacentrids in the Caribbean, if their courtship sounds are not distinguishable by pulse number or pulse rate. For these situations more complex analyses using sound localization by analyzing differences in time-of-arrival at multiple hydrophones could be used to obtain data on calling by individuals in groups (Spiesberger and Fristrup 1990).

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Table 1. Call detection accuracy. Comparison of the calls manually detected from a tape made of the detector input with the calls detected by the acoustic detector. Only channels 1 and 3 (Ch1 and Ch3) were used during the deployment (channel 2 and channel 4 were not used). False detections show the # sounds detected by the acoustic detector/# sounds manually detected from the tape.

\* Channel 3 was not operating on 24 April 1994.

\*\* For calls detected by both channels the call detected on channel 3 was louder than the calls detected on channel 1.

| | Hydrophone Input | Ch-3 (Male 2) | Ch-1 (Male 1) | Ch-1 (Male 3) | Ch-1 (Male 3) | Ch-1 (Male 3) |
|---|---|---|---|---|---|---|
| Tape Recording Information | Date | 4 April | 12 April | 17 April | 17 April | 24 April |
| | Time of Recording | 23:17 | 19:35 | 15:30 | 17:45 | 08:04 |
| | Minutes Analyzed | 45 | 45 | 45 | 45 | 11 |
| Calls Manually Detected on Tape | Proximate | 16 | 120 | 44 | 184 | 189 |
| | Background | 0 | 25 | 5 | 20 | 16 |
| Calls Detected by Acoustic Detector | Calls Detected Ch 1 | 10 | 72 | 44 | 108 | 169 |
| | Calls Detected Ch3 | 4 | 44 | 0 | 7 | \* |
| | Total # Calls Detected /Proximate Calls Manually Detected | 14/16 | 116/120 | 44/44 | 115/184 | 169/189 |
| | Background Calls Detected on Main Channel | 0/0 | 3/25 | 0/5 | 3/20 | 8/16 |
| | Calls Detected Both Channels | 2 \*\* | 0 | 0 | 2 \*\* | \* |
| False Detections | Hydrophone Bites | 0/0 | 0/3 | 0/0 | 5/16 | 0/0 |
| | Squirrelfish or Unknown | 0/25 | 0/21 | 0/0 | 0/0 | 0/0 |

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Table 2. Calling rates before and during one visiting event by one female to three males. The duration of the visiting event was 2.18 minutes. The time period before visiting was 13.27 minutes. Calling rate is calls/minute. The individual fish were not the same males monitored with the detector (i.e. males 1, 2, and 3).

| Fish | Before Visiting | | During Visiting | |
|---|---|---|---|---|
| | # Calls | Calling Rate | # Calls | Calling Rate |
| Fish A | 3 | 0.23 | 17 | 7.80 |
| Fish B | 0 | 0 | 10 | 4.59 |
| Fish C | 0 | 0 | 7 | 3.21 |
| Total | 3 | 0.23 | 30 | 15.60 |

Figure 1. Rate of sound production in calls/hour (squares, dotted line) and calls/day

(diamonds, solid line) and occurrence of eggs. Boxes below dates indicate days eggs were

present in a male's nest. The day of egg-laying is indicated by an 'S' in the box Labeled

tick marks are at 1200h. Unlabeled tick marks are midnight. Note the difference in scales

for A, B, and C.

A. **Male 1**

B. **Male 3**

C. **Male 2**

D. **Male 2**

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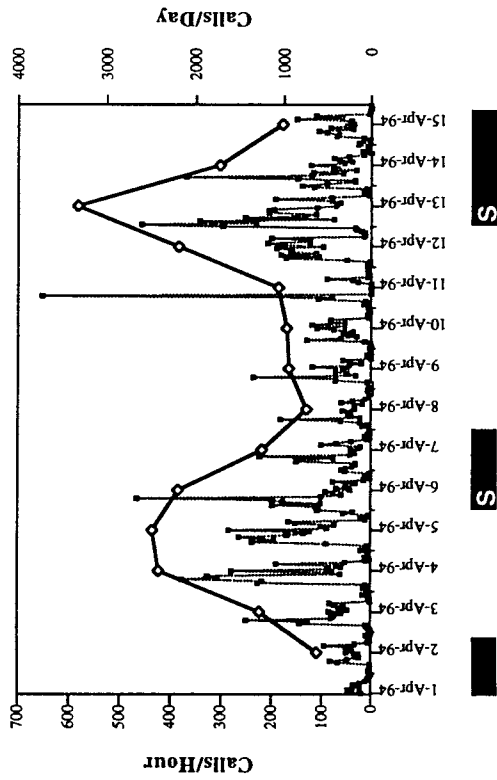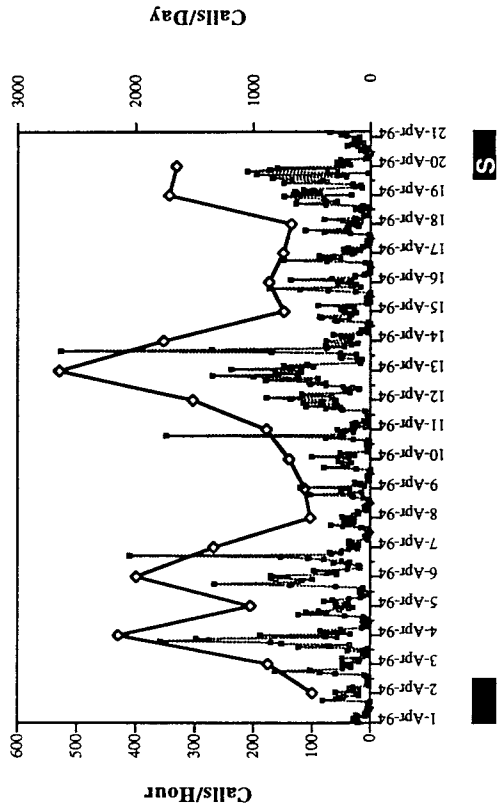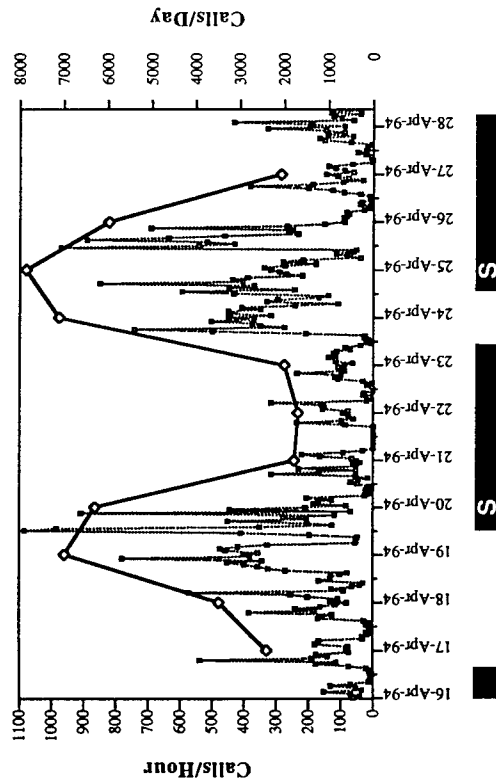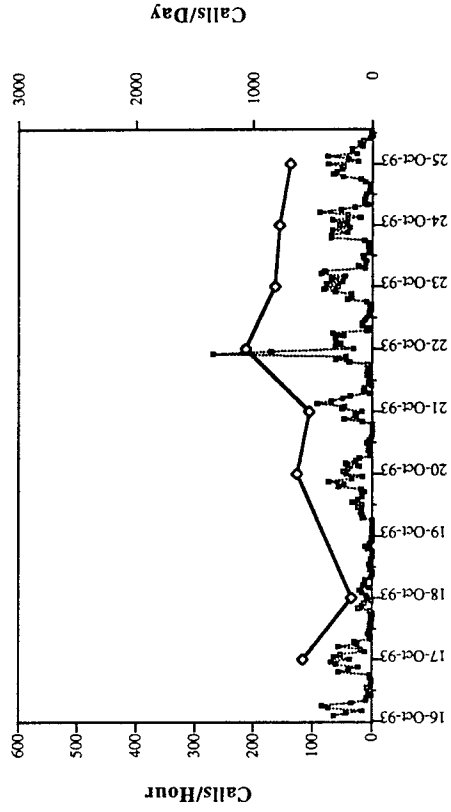
Figure 2. Rate of sound production in calls/10 minutes (solid line) plotted with irradiance (dotted line) for three individuals. Boxes below dates indicate days eggs were present in male's nest. The day of spawning is indicated by an 'S' in the box.

## A. Male 1



## B. Male 2



## C. Male 3



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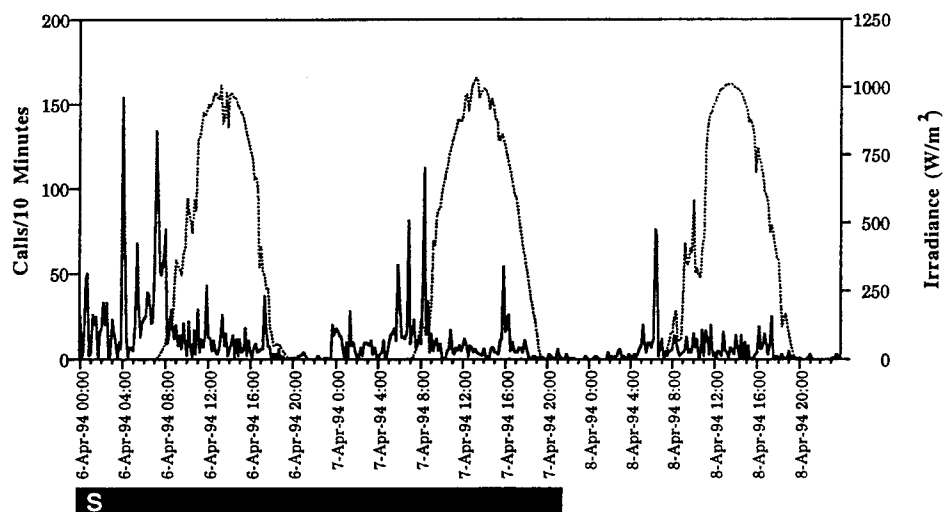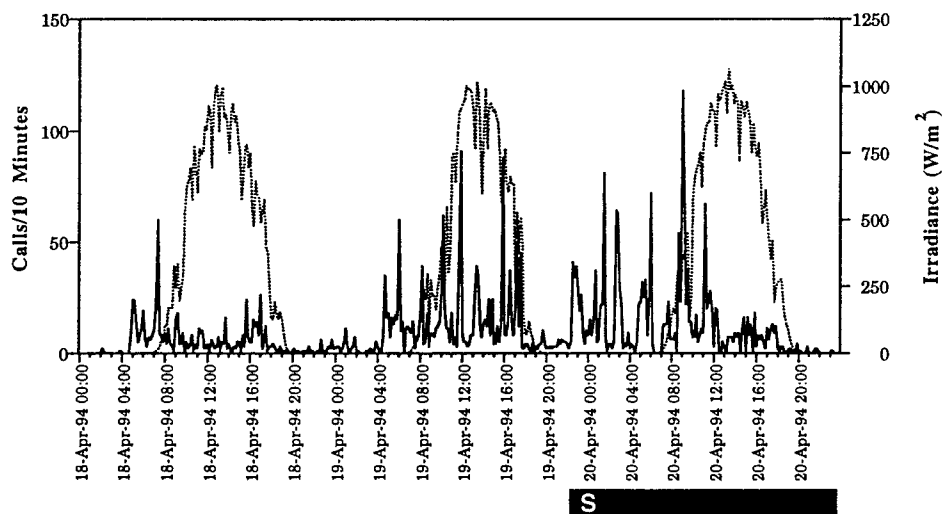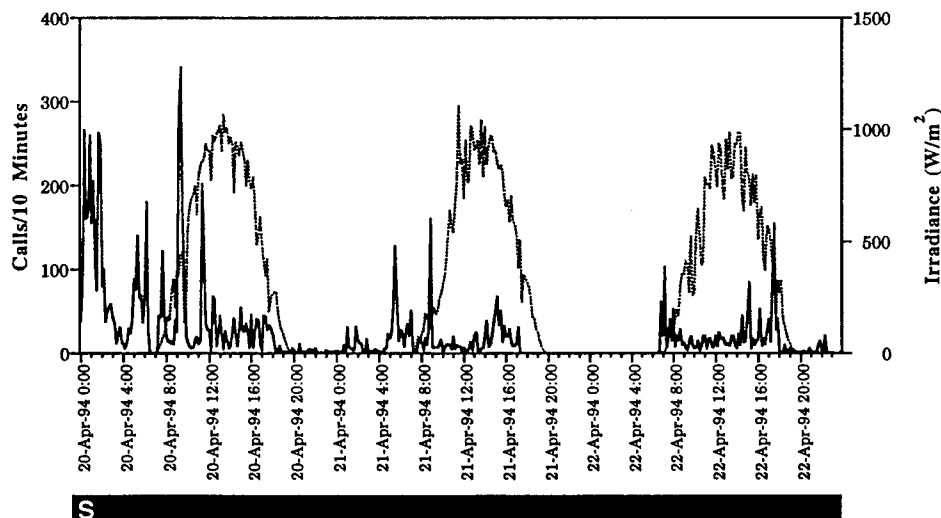
# Chapter V

# Female Mate Choice and Acoustic Cues in the Damselfish
*Dascyllus albisella*

## Abstract

Patterns of male reproductive success were studied in the damselfish, <u>Dascyllus albisella</u>. Reproductive success varied for individual males over successive reproductive cycles and was not correlated with male size. The variation in reproductive success suggests that females choose males based on characters that vary from cycle to cycle. In a previous study, a passive acoustic detector was used to continuously measure sound production; rates of courtship were positively correlated with reproductive success. The continuous time-series of sound production were analyzed to determine appropriate sampling strategies to measure male sound production. Short samples of sound production (10 minutes or 60 minutes per male per day) were poor estimators of peak calling rates and daily calling rates. The rich variation in male courtship rates may contain information about male condition that has been previously ignored.

Female mate choice in soniferous animals has been the subject of intense investigation in amphibians, insects, and birds, and features of male calls such as dominant frequency and call rate have been found to be used by females in mate assessment (e.g. Ryan 1985; Gibson and Bradbury 1985; and references within). Most damselfishes produce a pulsed sound during the signal jump, in which a male rises from the bottom and then swims down rapidly (Myrberg 1972; Lobel and Mann in press). The initial goal of this study was to determine the features of the courtship call females may use to choose mates by studying variation in call characteristics and male reproductive success.

The dominant frequency of the courtship call in damselfishes, and in frogs, is negatively correlated with male size (Ryan 1985; Myrberg *et al.* 1993; Lobel and Mann in press). Male size is positively correlated with male reproductive success in some fishes (Perrone 1978; Noonan 1983; Thresher and Moyer 1983; Cote and Hunte 1989; Gronell 1989; Reynolds and Gross 1992), but there are also many fishes for which this does not hold (Thresher and Moyer 1983; Itzkowitz and Makie 1986; Petersen 1989; Knapp and Warner 1991; Petersen 1995), or where the relationship is the result of differences in territory quality associated with male size (Hoelzer 1990). The reproductive success of males was examined to determine the pattern for <u>Dascyllus albisella</u>.

As with male size, courtship rate is correlated with male reproductive success in some fishes, but not others. The rate of courtship in damselfishes, and thus sound production, is positively correlated with male reproductive success in the damselfishes <u>Stegastes partitus</u> and <u>Chrysiptera cyanea</u> (Schmale 1981; Gronell 1989; Knapp and Kovach 1991; Knapp and Warner 1991). Two other studies found no correlation between reproductive success and courtship rates for the damselfishes <u>Hypsypops rubicundus</u> and <u>Stegastes rectifraenum</u> (Sikkel 1988; Hoelzer 1990). The rate of signal jumping may provide females with a reliable cue for male vigor that is predictive of subsequent brood survival (Knapp and Kovach 1991).

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Dascyllus albisella males and females are permanently territorial and spawn synchronously about once every six days (Danilowicz 1995). Females also visit male nests on the day prior to spawning, and male courtship dipping rate and sound production is intense during these visiting episodes (Mann and Lobel in press). In D. albisella females likely assess potential mates during visiting the day prior to spawning, but also could assess males over long time periods since they reside in the same territories from months to years. It is very difficult to sample male courtship rates continuously for six days using SCUBA.

Continuous data on the timing of sound production by three male D. albisella were measured using a passive acoustic detector (Mann and Lobel in press). These data showed that maximal calling rates (calls/10 minutes) were positively correlated with male reproductive success, although the sample size of males was small (Mann and Lobel in press). This continuous data record of sound production was analyzed to determine an appropriate sampling strategy to measure male calling rates, so that more males could be sampled.

## Methods

The study was completed at Johnston Atoll, Central Pacific Ocean (16°44.2' N, 169°31.0' W) from 13-26 July 1993, 15-21 February 1994, and 2-28 April 1994. Male Dascyllus albisella are site-attached and reside in specific coral heads (Danilowicz 1995). Coral heads with resident males were tagged with flagging tape at five sites. Fish were not tagged so as not to disturb them. Some individuals were identifiable by scars and missing scales, and did not move between coral heads. Two sites, Herbicide Orange (HO) and West End (WE), were studied over all of the time periods. Three additional sites at Buoy

14 (B14-1, B14-2, B14-3) were studied in February and April 1994. Males at WE and B14-2 were collected at the end of the study in May 1994. Standard length and blot-dry weight were measured and sex was verified.

Dives were made daily usually between 0800-1200 hrs at each of the five sites to assess male reproductive status. Presence or absence of broods was recorded. In April 1994 brood size was estimated by comparing the area of the brood to the area of my left hand, 186 cm$^2$. This method was adopted because eggs were laid in irregular patterns on a wide variety of substrates; for example, broods might be found on smooth or irregular surfaces on the outside or inside of coral heads. Male reproductive success in this study was defined as the area of eggs received.

Sound production of three males was monitored continuously at three coral heads at Buoy 14-2 using a passive acoustic detector. Data were collected from 1-15 April for male 34 (2 spawning cycles), 1-21 April for male 35 (3 spawning cycles), and 16-28 April for male 36 (2 spawning cycles). The passive acoustic detector detected approximately 96% of the calls for males 34 and 35, with less than 2% false detections of the calls of other individuals. The data for male 36 likely included calling by another male, so the level of correct detection could not be accurately estimated. For details on the detector see Mann and Lobel (in press). The data were binned into 10-minute, 1-hour, and daily bins. Ten-minute bins were chosen because they have been used in field studies and have been correlated with male reproductive success (Knapp and Kovach 1991; Knapp and Warner 1991; Mann and Lobel in press).

Randomization tests were performed to test whether differences in the probabilties of a male receiving a clutch of eggs was higher depending on whether he had a clutch the previous cycle. For each of the reproductive cycles the distribution of males with clutches was randomized, and a test statistic was calculated as:

$$\frac{m_{rpc}/m_{pc}}{m_{rnc}/m_{nc}}$$

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where:

$m_{rpc}$ =number of males that received a clutch that also had a clutch the previous cycle

$m_{pc}$ =number of males with clutches the previous cycle

$m_{rnc}$ =number of males that received a clutch that did not have a clutch the previous cycle

$m_{nc}$ =number of males without clutches the previous cycle

## Results

Male reproductive success varied over consecutive reproductive cycles (Table I). For example, comparing males 4, 5, and 6 in the first cycle of July 1993, males 4 and 6 received clutches of eggs while male 5 did not. On the second cycle males 4 and 5 recieved clutches, but male 6 did not, and on the third cycle male 6 received a clutch while 4 and 5 did not. The probability of a male receiving a clutch in April was higher at four out of five sites for males that did not raise a clutch the previous cycle (Fig. 1). However, none of these differences were statistically significant based on the results of randomization tests. There was no statistically significant correlation between male size and reproductive success in April 1994, measured as the number of broods or total area of eggs (Table II).

Figure 1 shows a portion of the sound-production time-series for males 34 and 35. Females spawned on 6 April during this cycle; male 34 received a clutch of eggs, while male 35 did not. Calling by male 34 was higher on 5 April, when female visiting was expected. The distributions of male calling rates were skewed to the right, and had large measures of skewness (Fig.2 and Table III).

Females might assess daily levels of male calling or burst calling rates. To determine how well daily levels of calling could be estimated by sampling for 10 minutes or

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1 hour per day, the number of calls per day was correlated to the number of calls per hour and calls per 10 minutes. These correlations were calculated for every hour of the day (for hourly samples) and for every 10 minutes (for 10-minute samples) to determine if some times of the day were better to sample than others (Fig. 4). The best time to sample would be between 0800 and 1100. The correlations using 10-minute sampling periods were on average lower than correlations obtained with 1-hour sampling periods (Table IV). There was no time of day that gave a consistently high correlation above 0.7 for all fish. If random 10-minute or 1-hour samples were used to estimate daily calling rates and there was a perfect correlation between calling rate and male reproductive success, the coefficient of determination ($r^2$) from the regression of estimated calling rate on reproductive success would only be 0.172 and 0.324, respectively (Table IV).

To determine how well the maximum burst calling rate per day (maximum calls/10 minutes) could be estimated without continuous sampling, correlations were calculated between the daily maximum burst calling rate and the number of calls in 10-minute and 1-hour sampling periods (Fig. 5a and b). The average correlation obtained with 10-minute samples was lower than that obtained with 1-hour samples, but both were below 0.1 (Table IV). The correlation between the maximum burst rate and its estimate using the maximum burst rate in a one hour sampling period was higher than ten minute or one hour samples (Table IV). If there was a perfect relationship between male burst courtship rates and reproductive success, estimates of burst courtship rates made by randomly sampling using these methods would yield coefficients of determination ($r^2$) less than 0.1 (Table IV).

# Discussion

This analysis showed that it would be very difficult to simultaneously sample the calling rates of several males using direct observation. Because the calling rates are sporadic, the time needed to sample each male adequately makes it impractical using SCUBA. In fact, none of the methods yielded satisfactory results. Thus, the original intent of this study, to determine which features of the courtship call are used in mate choice, will remain unfulfilled. Sullivan (1990) recognized the problems of sampling male characters over shorter periods of time than the female could sample. This study clearly demonstrates that variation in courtship rates for fishes need to be measured to assure that they can be accurately estimated from shorter samples. If there was a perfect linear relationship between courtship rate and male reproductive success, and courtship rates were estimated with random 10-minute samples, the resulting $r^2$-values of a regression would have been 0.172 for daily calling rates and 0.007 for burst calling rates.

Whatever characteristics female <u>Dascyllus albisella</u> might use to choose mates, they clearly change over successive spawning periods. Size does not play a role in female choice for the size ranges used in this study, as in most other studies of damselfishes (Petersen 1995). The coefficient of variation of male reproductive success (20 percent) was lower than all other damselfishes that have been studied, which all had CV's greater than 30 percent (Petersen 1995). This may be due to less variability between males of <u>D. albisella</u> and/or a difference in female mate choice behavior.

Seven out of 51 males (13.7%) disappeared during this study, but no females disappeared. All but one of the disappearances took place over periods when there were breaks in observation, so it is possible that the males moved to other areas. A jack (<u>Caranx melampygus</u>) was seen rapidly swimming around the coral head at the time of disappearance of one male, and possibly had attacked the male. If these disappearances were the result of predation, then there could be a high cost to performing the signal jump. This is supported by data from <u>Dascyllus aruanus</u> (which is about two-thirds the size of <u>D.</u>

<u>albisella</u>), in which 11 out of 24 cases of predation were on displaying males (Shpigel and Fishelson 1986).

A passive acoustic detection system with many detectors could be used to continuously monitor calling rates of individual males to test what features of courtship females may choose. While continuous data series solve the problem of undersampling, they raise the issue of what feature or features females may use to make mating decisions. The continuous time-series of courtship rates presents a much richer view of damselfish behavior than 10-minute samples. We have analyzed the time-series in terms of daily courtship rates and burst rates in ten-minute bins, but females could be interested in other features of courtship such as bout length. Analysis of continuous time-series from more males and species will help answer these questions.

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Table I. Nest status of males at five sites over consecutive spawning cycles in three different months.
The actual date of the cycles are not neccesarily the same between sites. Therefore, some sites have more cycles than others.
x indicates male with brood.  o indicates male without brood.
Male gone means male disappeared from his territory.

| Site | Male | Jul 93 | | | Feb 94 | | Apr 94 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| WE | 1 | x | x | x | o | x | x | x | x | x | x |
| | 2 | x | o | o | o | o | o | o | x | x | o |
| | 3 | x | o | o | x | x | x | o | x | x | o |
| | 4 | x | x | o | o | o | male gone | | | | |
| | 5 | o | x | o | x | x | o | x | x | male gone | |
| | 6 | x | o | x | male gone | | | | | | |
| | 7 | o | x | x | x | x | x | x | x | x | x |
| | 8 | x | x | x | o | x | o | x | o | x | x |
| | 9 | x | x | x | x | x | x | x | x | x | x |
| | 10 | x | o | x | o | x | x | x | x | x | x |
| | 11 | o | o | o | male gone | | | | | | |
| | 12 | o | o | x | o | x | x | x | x | x | x |
| HO | 13 | x | o | | x | | x | x | o | x | o |
| | 14 | x | o | | o | | x | x | x | x | o |
| | 15 | | | | o | | o | o | o | x | o |
| | 16 | x | x | | x | | x | x | x | x | o |
| | 17 | x | x | | x | | x | o | x | o | x |
| | 18 | x | o | | male gone | | | | | | |
| | 19 | x | o | | x | | x | x | o | x | x |
| | 20 | x | o | | x | | x | o | x | x | x |
| | 21 | o | x | | x | | male gone | | | | |
| | 22 | | | | x | | o | x | o | x | x |
| B14-1 | 23 | | | | o | x | x | x | x | x | x |
| | 24 | | | | x | x | o | x | x | x | o |
| | 25 | | | | | | o | x | x | o | x |
| | 26 | | | | o | o | o | x | o | x | x |
| | 27 | | | | o | x | o | x | x | x | x |
| | 28 | | | | | | o | x | x | x | x |
| | 29 | | | | x | o | o | o | x | o | o |
| | 30 | | | | | | o | x | x | x | o |
| | 31 | | | | o | o | o | o | x | o | o |
| | 32 | | | | x | x | x | x | x | o | x |
| | 33 | | | | x | x | o | o | x | o | x |
| B14-2 | 34 | | | | x | | x | x | x | x | x |
| | 35 | | | | x | | x | o | o | x | x |
| | 36 | | | | x | | x | x | x | x | x |
| | 37 | | | | o | | o | x | o | x | x |
| | 38 | | | | x | | o | x | x | x | x |
| | 39 | | | | x | | o | x | x | o | x |
| | 40 | | | | x | | male gone | | | | |
| | 41 | | | | x | | x | x | o | x | o |
| B14-3 | 42 | | | | x | | x | o | o | x | x |
| | 43 | | | | o | | o | x | o | o | x |
| | 44 | | | | o | | o | o | x | o | o |
| | 45 | | | | o | | o | x | x | o | x |
| | 46 | | | | o | | o | x | o | x | x |
| | 47 | | | | o | | o | o | o | x | x |
| | 48 | | | | o | | o | o | x | x | x |
| | 49 | | | | o | | o | x | o | x | o |
| | 50 | | | | o | | o | x | o | o | x |
| | 51 | | | | o | | o | x | o | o | x |

Table II. Spearman correlation (r) and p-values of male weight and reproductive success (total number of nests and relative egg area) at two sites.

| Site | n | Number Nests | | | | Relative Egg Area | | | | | Male Weight (g) | |
|------|---|---|---|---|---|---|---|---|---|---|---|---|
| | | r | p | Mean | SD | r | p | Mean | SD | CV | Mean | SD |
| West End | 7 | 0.06 | 0.90 | 4.0 | 1.3 | -0.21 | 0.65 | 6.7 | 1.3 | 19.4 | 35.5 | 7.2 |
| Buoy | 14 | -0.35 | 0.35 | 3.7 | 0.4 | -0.64 | 0.12 | 6.4 | 1.3 | 20.3 | 45.1 | 2.6 |

Table III. Descriptive statistics of calling rates (calls/10 minutes) by three males.

|          | Male 1 | Male 2 | Male 3 |
|----------|--------|--------|--------|
| n        | 2153   | 2916   | 1795   |
| Mean     | 11     | 8      | 28     |
| Median   | 4      | 4      | 14     |
| Skewness | 10.7   | 7.9    | 25.1   |

Table IV. Statistical results of correlation analyses averaged for three males. $X_{corr}$=mean of correlations. $SD_{corr}$ = SD of correlations. $r^2$= coefficient of determination of a regression of the estimated calling rate versus male reproductive success, if there was a perfect relationship between the true calling rate and male reproductive success.

| Sampling Time | Calling Rate Estimated | Range of Correlations | | $X_{corr}$ | $SD_{corr}$ | $r^2$ |
|---|---|---|---|---|---|---|
| 10 min | Daily | -0.352 | 0.955 | 0.414 | 0.227 | 0.172 |
| 1 hr | Daily | 0.146 | 0.845 | 0.569 | 0.153 | 0.324 |
| 10 min | Max. Daily Burst | -0.638 | 0.935 | 0.064 | 0.273 | 0.004 |
| 1 hr | Max. Daily Burst | -0.443 | 0.832 | 0.086 | 0.289 | 0.007 |
| Maximum rate in 1 hr | Max. Daily Burst | -0.472 | 0.913 | 0.270 | 0.297 | 0.073 |

Figure 1. Probability of receiving a clutch of eggs based on whether the male had a clutch the previous cycle in each of five sites. P-values test whether the probabilities are significantly different and are the result of randomization tests with 100 randomizations.

Figure 2. Continuous time-series of calls/10 minutes for males 34 and 35. Male 34
received a clutch of eggs on 6 April.
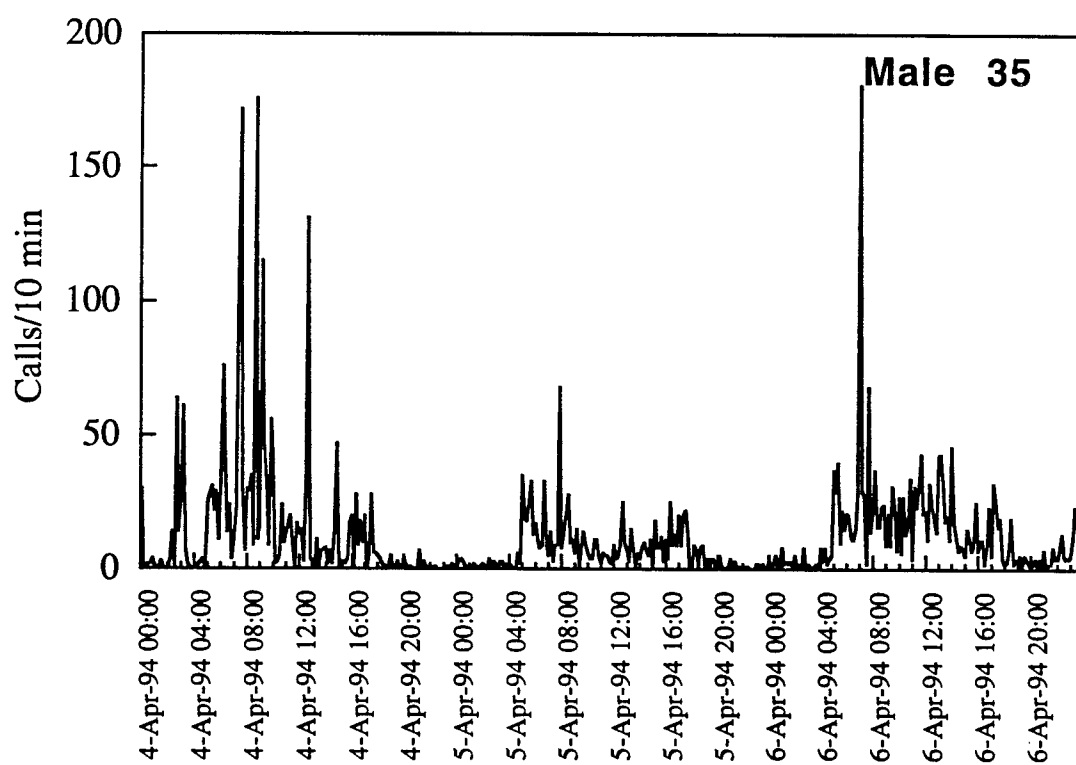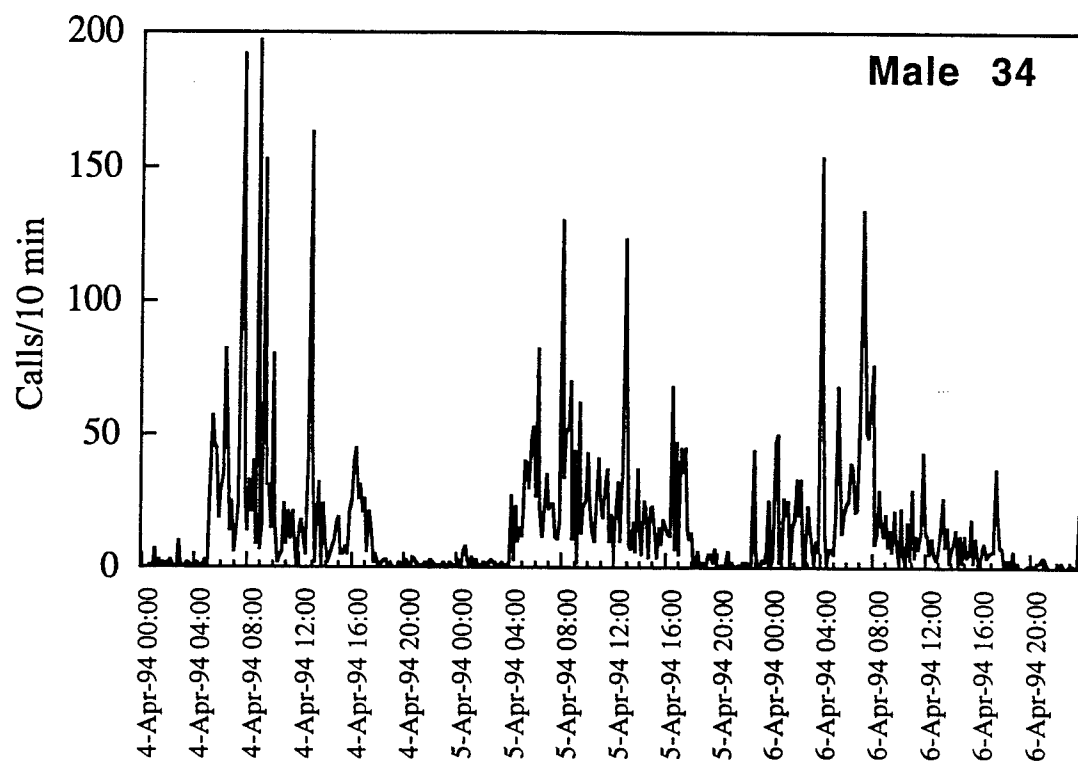
Figure 3. Distribution of call rates (calls/10 min) for males 34, 35, and 36. Inset figures have expanded ordinates.

Calls/10 min
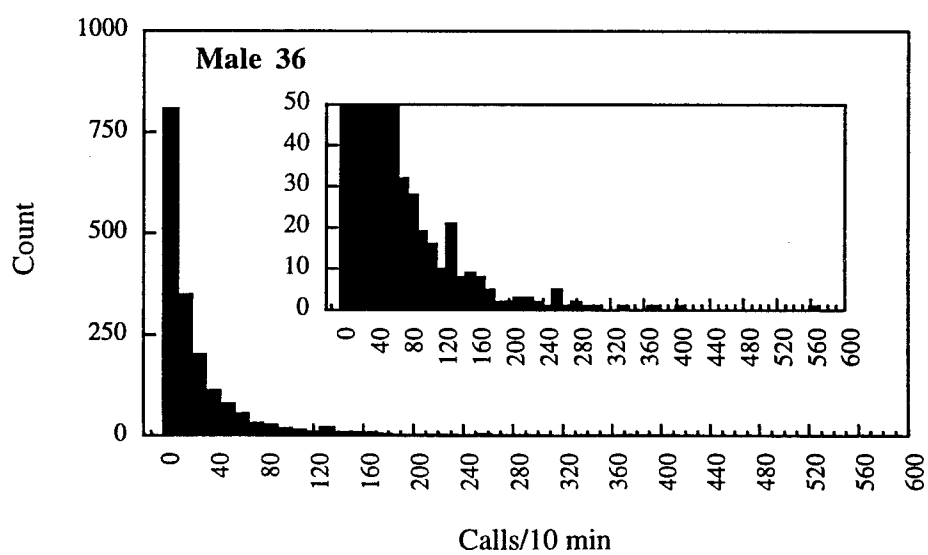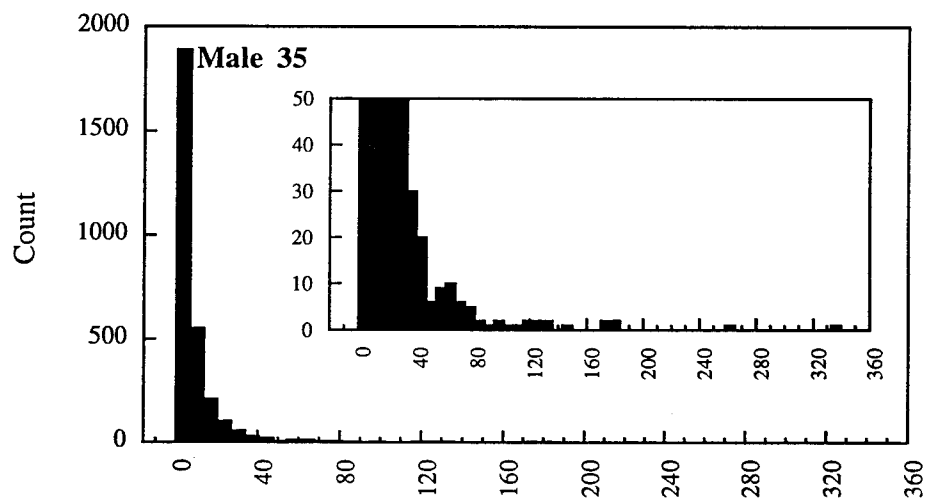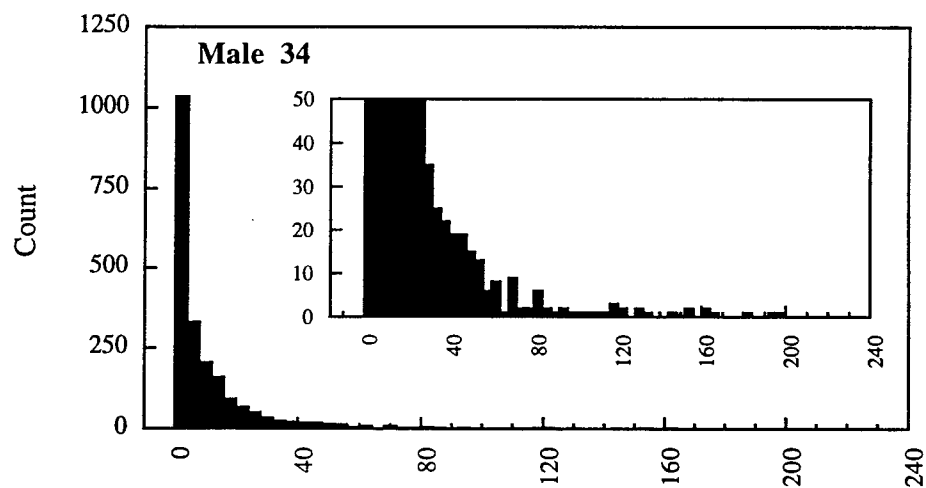
Figure 4. Correlation between total calls per day and estimated value obtained by sampling call rate in (a) one-hour samples and (b) 10-minute samples. Male 34 (squares). Male 35 (triangles). Male 36 (circles).
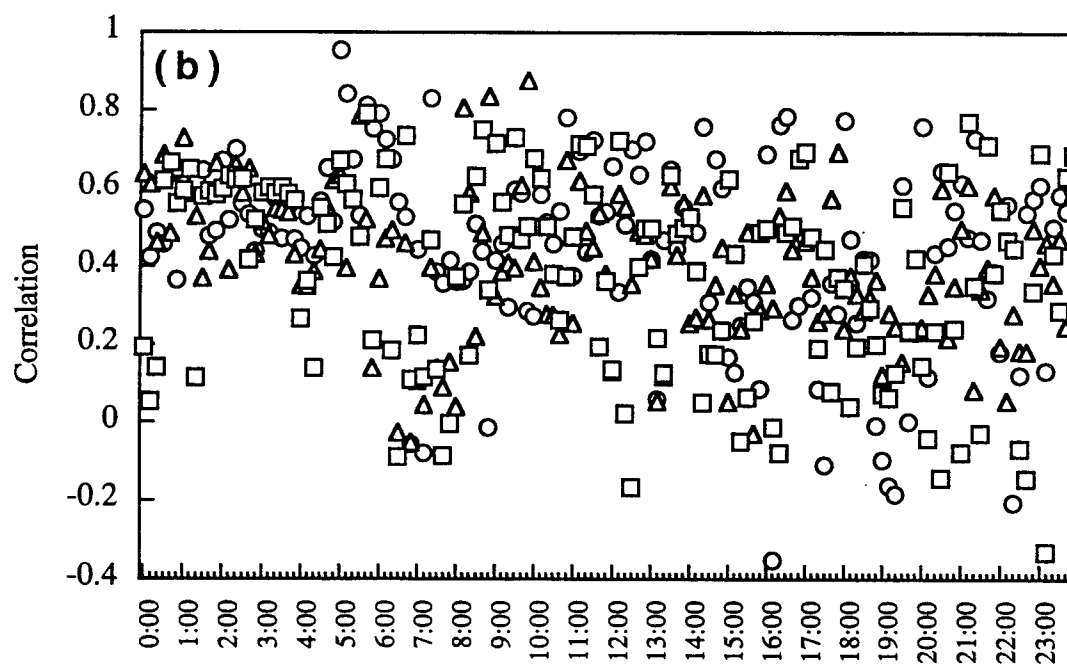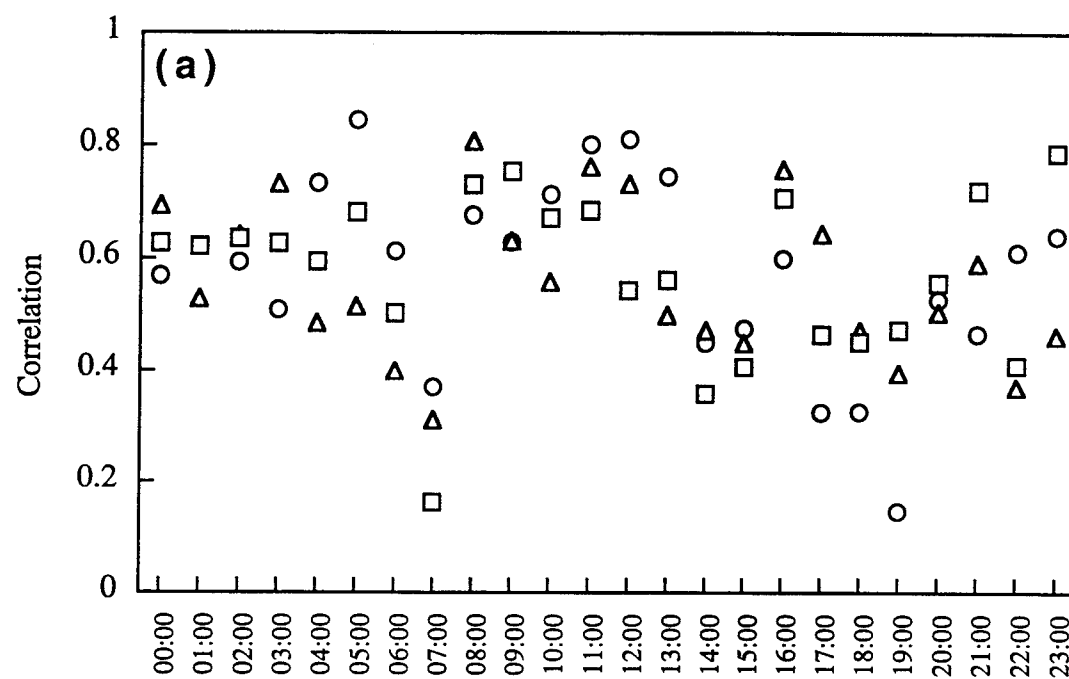
Figure 5. Correlation between daily maximum burst calling rate (calls/10 minutes) and estimated rate obtained by (a) 10-minute samples, (b) one-hour samples, and (c) maximum burst rate in one-hour samples. Male 34 (squares). Male 35 (triangles). Male 36 (circles).
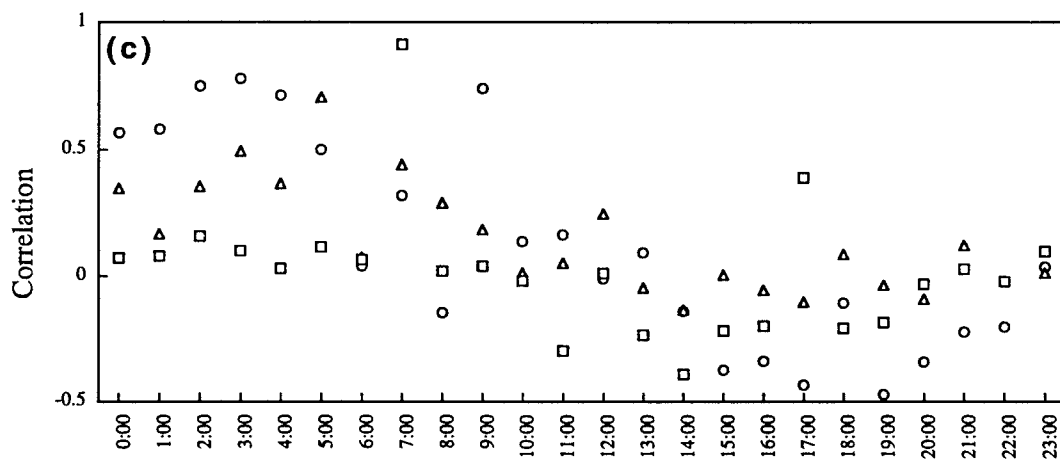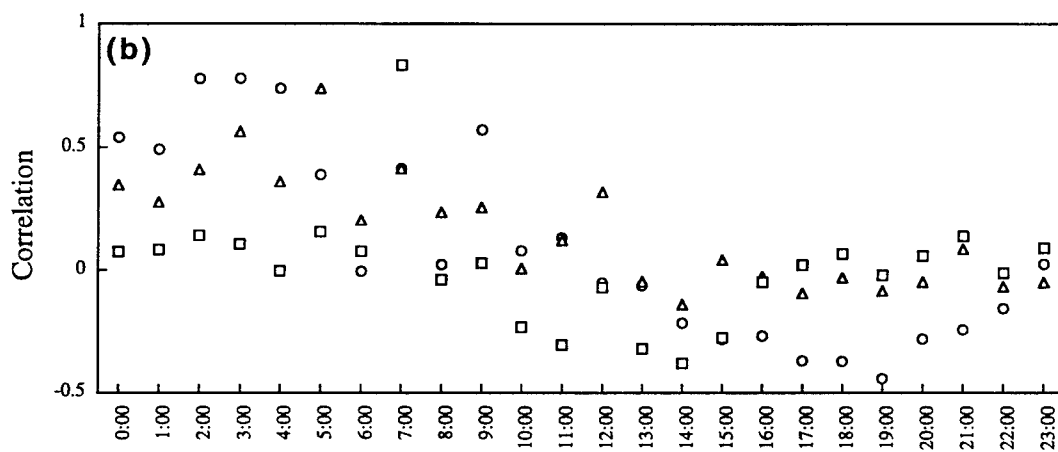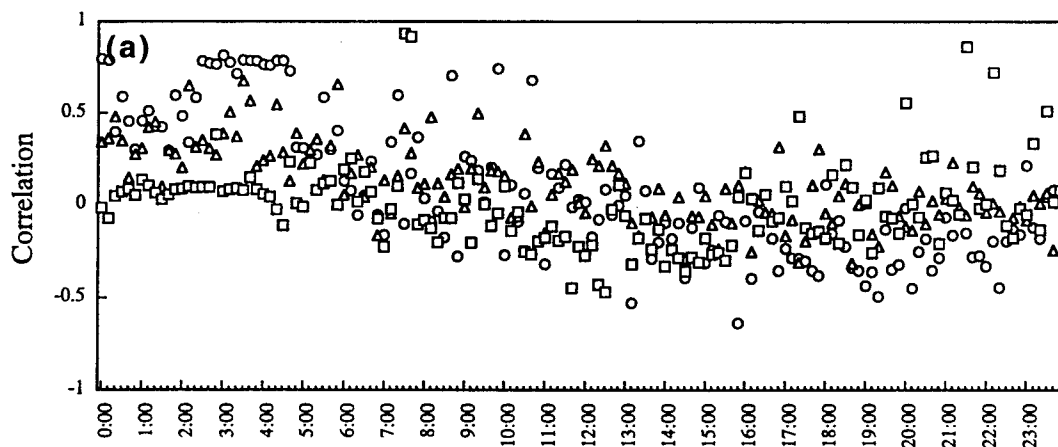
# Chapter VI

# Reproductive  Synchrony  in  Damselfishes

# Abstract

Damselfishes show a broad spectrum of reproductive synchrony, but it has been difficult to quantify since they reproduce continuously, as opposed to seasonally. Two measures of synchrony were developed and used in randomization tests to test for within-site reproductive synchrony of the damselfish, Dascyllus albisella, at Johnston Atoll, Central Pacific Ocean. Reproductive synchronization was localized to groups of fish on the order of 10-20 m. Reproduction was not synchronized at larger scales where groups were not contiguous. Average clutch size was larger on unsynchronized days, but there was no statistically significant difference between synchronized and unsynchronized days in the number of broods that prematurely disappeared or broods that contained non-developing eggs. To obtain quantitative data on spawning synchronization in damselfishes, synchrony indices were calculated for 10 species and tested for statistical significance using randomization tests. The results showed that the anemonefish, Amphiprion clarkii was least synchronized and Dascyllus albisella and Abudefduf troschelii were most synchronized. Viable hypotheses for the evolution of reproductive synchrony in Dascyllus albisella include 1) it is an evolutionary relict that is no longer selected for and possibly maladaptive, 2) it evolved as part of the haremic lifestyle of the common ancestor of the Dascyllus genus, and 3) there is selection pressure for synchronization during the larval stage.

## Introduction

Reproductive synchrony is well-known in marine fishes as well as many plants and animals (Ims 1990, Robertson *et al.* 1990). In fishes it is commonly based on lunar or semilunar cycles, although there are many cases of sublunar synchronization (Robertson et al. 1990). Lunar reproductive synchrony in organisms with planktonic larvae has been hypothesized to enhance the transport of larvae from the adult habitat to the open ocean (Christy 1978, Johannes 1978, Foster 1987). However, the high variability among many closely related species in the timing of reproduction relative to tides does not support this as general benefit of reproductive synchrony (Robertson et al. 1990). Evidence for benefits of synchrony in fishes include reduced filial cannibalism (Petersen and Hess 1991) and decreased predation on eggs (Foster 1989, Foster 1987). In other taxa synchronous reproduction has been correlated to reduced nest predation (snow geese) (Findlay and Cooke 1982), increased foraging efficiency of socially-foraging young (bank swallows) (Emlen and Demong 1975), and reduction in predation on newborns (ungulates) (Rutberg 1987).

To understand the evolution of reproductive synchrony it is necessary to compare levels of reproductive synchrony in many species (e.g. Rutberg 1987). Synchrony measures have been developed for seasonally reproducing organisms, including variance around a mean reproduction date (Emlen and Demong 1975, Findlay and Cooke 1982, Wiklund 1984) and birth-season lengths (Rutberg,1987). These measures are difficult to apply to continually reproducing organisms, like damselfishes and other tropical organisms, which may have several peaks in reproductive activity within one season. In damselfishes the number of days of reproductive activity per month (Foster 1987), and the autocorrelation of a time-series of spawning activity (Danilowicz 1995) have been used as measures of synchrony. Each of these measures has obvious deficiencies. The number of

days of reproductive activity is the same for 100 males spawning evenly over 10 days as for 90 males spawning on one day and the other 10 males spawning over 10 days. The same autocorrelation can be obtained for for 100 males spawning on 1 day every 10 days, as 100 males spawning over 4 days every 10 days (as long as the distribution was the same each cycle). A flexible measure of synchrony is required to allow comparisons between species in order to study its evolution. Furthermore, statistical tests are needed to test whether reproduction is synchronous.

We analyzed reproductive synchrony in five sub-populations of the damselfish, Dascyllus albisella. Two measures of reproductive synchrony were developed, one based on correlations between the brood status of males (the brood correlation method) and the other based on the time-series of spawning for all males (the spawning date method), and used in randomization tests to test for within-site synchronization. We followed the traditional paradigm in searching for the adaptive significance of synchrony, by comparing hatching success with the level of synchrony. Finally, we applied spawning date synchrony index to previously published time-series of reproduction in several damselfishes and interpreted reproductive synchrony in D. albisella using a phylogenetic framework.

## Methods

The study was carried out at Johnston Atoll (16°44.2' N, 169°31.0' W) from 13-26 July 1993, 9 October-4 November 1993, 15-21 February 1994, and 2-28 April 1994. Coral heads with resident males were tagged with flagging tape at five sites. Two sites, Herbicide Orange (HO) and West End (WE), were studied over all of the time periods. Three additional sites at Buoy 14 (B14-1, B14-2, B14-3) were studied in February and April 1994. (As a side note to satisfy the curious reader, Johnston Atoll is a United States military base that was used for the storage of herbicide orange in the 1970s. Some of this

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herbicide leaked on land, and probably into the ocean. The HO site in this paper is adjacent to the former storage site on land).

The locations of the tagged coral heads were mapped by measuring distances and compass bearings between adjacent heads. Daily dives were made usually between 0800-1200 at each of the sites to assess male reproductive status. Presence or absence of broods was recorded, except in April 1994 when brood size was estimated by comparing the size of the brood to my left hand, which is 186 cm$^2$. This method was adopted because eggs were laid in irregular patterns on a wide variety of substrates; for example, broods might be found on smooth or irregular surfaces on the outside or inside of coral heads. The fish failed to use artificial nesting surfaces including flower pot halves, floor tiles, and ceramic tiles that other damselfish species readily adopt (e.g. Robertson et al. 1990, Itzkowitz 1991).

Normally developing zygotes took four days to develop. They were cloudy on the day they were laid, clear on days two and three, and clear with a black embryo evident on day four. Zygotes that were not viable turned opaque white on day two, and often turned orange by day four.

Temperature measurements were made using temperature loggers at sites B14-2 and WE at 4m depth (XL-100 and TG-205 loggers, Braencker Research, Toronto, Canada). Loggers were calibrated using a mercury thermometer accurate to 0.1° C.

Synchrony indices and randomization tests were programmed using QuickBasic (Microsoft) on an Apple Macintosh. The tests and measures of synchrony will be described in the results.

Scientific nomenclature for damselfishes followed Allen (1991).

# Results

## Site Descriptions

The positions of the sites and male territories within each of the sites are shown in figure 1. Each of the sites is characterized by patch reefs with intervening areas of sand. The sites at B14 were chosen because they likely experience the same current patterns, temperature, and food regimes, yet were separated by continuous patches of corals rising to the surface that minimized the likelihood of fish moving between sites.

## Reproductive Behavior

Males and females shared territories and none changed their territories during the census periods. Males cleaned debris from a solid surface, usually dead coral, one to two days before spawning with females. Females visited males the day prior to spawning and inspected the nests of several males. During the visiting behavior, females swam over open expanses of sand to neighboring males and swam over the nest site with the male. The excursions are shown in figure 1 as lines connecting coral heads. Spawning took place from dawn to as late as 13:00, but was usually completed by 08:00. The start of spawning was never observed.

The pattern of reproduction is shown in figure 2, along with water temperature. There was no reproduction at any site from 9 October-4 November 1993. Autocorrelations calculated for each site in April had significant lags at 6 days for all sites, except for B14-3, which had a lag of 5 days ($\alpha$=0.05). Since the time for zygote development from laying until hatching lasted four days, there were usually two days with no zygotes between successive broods. There was no significant correlation between spawning and average daily water temperature at any of the sites in July 1993 or April 1994 ($\alpha$=0.05, Spearman rank correlation).

## Measures of Reproductive Synchrony and Randomization Tests

To test whether there was reproductive synchronization within the study sites, a synchrony index was calculated for each site and used in a randomization test in which this synchrony index was compared to the synchrony index obtained after the locations of the males were randomized among sites.

## Brood Correlation Method

For the correlation-based synchrony index, a time series for each fish was constructed based on whether the fish had a brood (1) or not (0). The data from July, February, and April were combined into one time series. The synchrony index for each site was then calculated as the average of all pairwise product-moment correlations of the brood time-series within each site. The average of the synchrony indices of the sites was compared to the same measure after randomization of the location of the fish. To test whether there was within-site synchronization, all sites were used in the randomization test. Out of 1000 randomizations, 0 produced a higher correlation than the unrandomized data, indicating that spawning was synchronized within sites (p<0.001).

The brood correlation method was also used to test for within-site synchronization between pairs of sites (Table 1). 7/10 of these tests produced significant results (p<0.05). The adjacent sites at B14 showed significant within-site synchronization, except B14-2 with B14-3, which was marginally significant (p=0.065).

The lack of statistically significant synchronization within some of the sites and inspection of the time-series suggested that there may be some sub-site synchronization. Based on the biology of the fish it would be most appropriate to define sites based on patterns of female visiting, including all males within the area visited by females. However, the data on female visiting was not extensive enough to allow this to be used as a criterion. At HO, WE, and B14-1 there were some males that were clustered, with other males scattered farther away. These sites were divided into subsites including the fish

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enclosed by ovals in figure 1. The randomization tests were performed using these subsites (Table 2). The test of WE and B14-3 was now significant (p<0.01), while that of HO and B14-2 was still not significant (p=0.44). Furthermore, other comparisons became less statistically significant (HO-B14-1, HO-B14-3, WE-B14-3).

## Spawning Date Method

The spawning date method was adapted from the method used by Petersen and Hess (1991). In this case a time-series for each male was generated using '1' for days a clutch of eggs was received, and '0' for all other days. The time-series for all males within a site were then summed to produce one time series per site. These are the same as the time series shown in figure 2. A day is defined as a synchronized day of spawning using the following rules:

1. Start with the first day. If it is equal to zero, then go to the next day. If it is greater than zero, then goto step 2.

2. Pick the day with the greatest number of broods over the next four days, this is defined as a synchronized day (since the zygotes took four days to develop until hatching, a neighborhood of four days was used to find the peak in spawning).

3. Begin the search for the next synchronized day four days later, and continue until the end of the time series is reached.

4. An out-of-synchrony score is calculated by summing the number of broods laid out of synchrony, and weighting each by the number of days to the closest synchronized day. The level of synchrony is then calculated as (out-of-synchrony score/total broods). Lower scores indicate higher synchronization.

Since this method is based on the temporal relationship among consecutive spawning dates, data sets from different time periods could not be combined. Randomization tests were performed with the nesting data from April. Randomizing

among all of the sites showed that spawning was synchronized within sites (p<0.001; 1000 randomizations). The pairwise comparisons of sites are shown in Tables 3 and 4. 5/10 of the randomizations were significant using all of the fish in each of the sites. When the subset of fish were used, 9/10 of the randomization tests were significant. Among the neighboring sites at B14, all showed within-site synchronization.

The synchrony indices obtained using the brood correlation and the spawning date methods are listed in Table 5 using the time-series data from April. The greatest difference in results is at WE. This difference is reduced when the WE subsite is considered.

## Reproductive Synchrony and Reproductive Success

To test whether the level of synchronization at a site was correlated with reproductive success, variance in reproductive success, nest disappearance, the number of females, or sex ratio, correlations were calculated between these factors and the spawning date synchrony index. While several of these correlations were high, when the subsites were used instead of the sites, none of the correlations held. They were sensitive to how sites were defined.

The relative success of broods laid on synchronized versus unsynchronized days was analyzed for each of the sites. Average clutch size was larger on unsynchronized days than on synchronized days, although the difference in means was not statistically significant (p=0.074 two-way ANOVA ; $Mean_{synch}=1.895\pm0.490$, $Mean_{unsynch}=2.395$ $\pm1.282$). The correlation between clutch size and percentage of males receiving a brood was low, inconsistent in sign between sites, and not statistically significant (Table 6). The percentage of broods containing non-developing eggs and broods that prematurely disappeared were both higher for broods laid in synchrony (Table 7), although neither was statistically significant ($\alpha=0.05$, $x^2$-test). Premature disappearance was rare. On two occassions the damselfish, <u>Abudefduf sordidus</u>, was observed attacking and completely

eating D. albisella nests.  Filial cannibalism was never observed, and bite marks indicative of partial clutch cannibalism were never observed.  The estimated clutch size never decreased during brooding, unless the entire brood disappeared.  However, stomach contents of D. albisella collected for other experiments revealed the presence of damselfish eggs.

The only case of multiple broods laid on different days in one nest was at WE on the spawning cycle following the loss of one male, when two broods were laid on consecutive days in one nest.


## Reproductive Synchrony in other Damselfishes

Time-series data of reproduction in other damselfishes were taken from the literature (Figure 3).  Since the time series for each male was unkown, the correlation index could not be calculated.  The spawning date method was used to calculate synchrony indices.  Since these species have different brood incubation times and different periods of cycling (as calculated by autocorrelation), the spawnning date method was modified to calculate several indices using different window lengths, from two to (cycle period/two) days, to identify peak spawning dates (step two of the rules for calculating the spawning date synchrony index).

To investigate the effects of using different window lengths, a random time series was generated by randomly choosing from 0-9 spawnings for 100 days, and an "unsynchronized" time series was generated by filling 100 days with 10 spawns per day.  The synchrony indices for these time series were calculated using window lengths of 2 to 50 (Figure 4).  The step features of the synchrony indices are due to the finite length of the time-series. The step size increases as the window length approaches the length of the time series.  The relationship between synchrony index and window length for an infinite length "unsynchronized" time series was calculated to be :

Synchrony index= Window Length/4

Since larger windows produce larger synchrony indices, the synchrony indices for the damselfishes were scaled by dividing the unsynchronized time-series index by the indices for each species. This scaled synchrony index is larger with greater synchronization. Three synchrony indices were calculated for each species using window lengths based on cycling period/2, the number of days to hatch-1, and the window that maximized the index (Table 8).

A randomization test was developed to test for the significance of these indices by comparing them to the same index calculated after randomizing the time series by randomly distributing the spawning events over the number of days of observation. The results of the randomization tests are shown in Table 8.

## Discussion

### Synchrony measures

Both the brood correlation and spawning date methods were useful in testing for reproductive synchronization. The main advantages of the brood correlation method is that is can be applied to non-continuous time series and it does not require the windowing that is used by the spawning date method. The spawning date method is only applicable to continuous time series.

The largest drawback of applying these techniques to the number of broods or spawns obtained by males is that they are influenced by the variance in reproductive success of the males. The variance in male reproductive success explains the different results obtained with the two methods for D. albisella (Table 8). Egg-laying by females should be measured to accurately measure reproductive synchrony. Damselfishes are

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among the best-studied reef fishes, because it is easy to survey the nests of many males at several sites. The laying activity of females is much more difficult to measure at several sites because they spawn over a period of hours. By studying the males we are estimating the number of females reproducing. The accuracy of this estimate is directly related to the variance in success of males in obtaining broods.

## Potential Mechanisms of Synchrony and Importance for other Studies

Since the neighboring sites at B14 were independently synchronized, it is likely that some social mechanism is driving synchrony. If an environmental factor is important in determining the pattern of spawning, it must be very subtle and will likely prove difficult to study.

Our data suggest that the scales of synchronization at Johnston Atoll were on the order of 10-20m, since the sites at B14 were independently synchronized. Danilowicz (1995a) found that spawning in D. albisella in Hawaii was synchronized at scales less than one km, but unsynchronized on larger scales. However, data from two transects within a small area had a cross-correlational lag of -1 days. The largest this lag could be is three days, since they spawned cyclically every six days. We suggest that this shows that spawning was not synchronized at scales less than one km.

At larger scales in Hawaii, reproduction was occasionally synchronized in association with changes in water temperature (Danilowicz, 1995b). Although our data are not nearly as extensive, there was no evidence for large-scale synchronization at Johnston Atoll in July, February, or April, and there was no correlation of spawning intensity to water temperature. This could be due to the warmer temperature of Johnston Atoll, which does not experience as drastic a change in temperature with seasons as Hawaii (DM

unpublished data). It is also possible that this large-scale synchronization is a random occurrence, since spawning was cyclic with a six day period.

Chemical, visual, and acoustic cues could all be important in synchronization. Males produce a sound during the signal jump, which is easily audible and visible over the range of synchronization seen in this study, and the rate of signal jumping changes with the spawning cycle (Mann and Lobel in press). The relationship between the signal jump and the spawning cycle has also been observed in Dascyllus trimaculatus and Dascyllus marginatus, both of which spawn in synchrony (Fricke 1973, Holzberg 1973). Although the signal jump seems to be a cue that could be used for synchronization (Fricke 1973), it could reflect a response to a less obvious female cue, such as a pheromone. There is evidence that such a process could be important in the bicolor damselfish Stegastes partitus in which males courted only when water from tanks containing females was added to their aquarium (Kenyon 1994).

The relationship between spawning patterns and recruitment have been used to make inferences about planktonic processes. But since only a few sites are used to study reproduction, it is difficult to know if the same pattern holds over the entire reproductive population (Robertson et al. 1988, Meekan et al., 1993). In D. albisella at Johnston Atoll, there appears to be the same seasonality in reproduction at different sites, but on a daily basis, the timing of reproduction is widely varying, making measurement of reproduction at one site a bad estimator of population reproduction.

## Adaptive Value of Synchronization

Adaptive can mean two different things. It is most often used in the sense of an evolutionary adaptation--that an organism has responded to selective pressures and adapted to a particular environmental variable (Futuyma 1986, Harvey and Pagel 1991). It is also, though more rarely, used to describe learning by an organism. By studying correlations of

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reproductive synchrony with reproductive success, we are measuring the current selective pressures for synchrony, not adaptation in either sense. Most authors, however, infer that if there are selective pressure for synchrony and they measure some level of synchronization, then synchrony must have evolved as a result of this selective pressure. This is a theoretical leap that would be better supported by using comparative data. A good example is the study by Foster (1987) who showed higher levels of synchrony associated with egg predation in <u>Abudefduf</u> <u>troschelii</u> compared to its sister-species <u>Abudefduf</u> <u>saxatilis</u>.

For <u>D. albisella</u> there appears to be no current selection for synchronization. If anything, there is a selective disadvantage of synchrony in brood size, brood loss, and failure to develop. There is little evidence of filial cannibalism, or predation by other fishes on <u>D. albisella</u> broods (this study and Danilowicz 1995). We were unable to measure the selective pressures for synchronous hatching of larvae. It is currently impossible to study mortality of specific planktonic larvae, thus any reduction in predation or increase in feeding abilities due to synchronous hatching of larvae in one area can not be measured. This is potentially very important, and techniques to study it are sorely needed.

Modelling has suggested that females may use reproductive synchrony to enforce parental investment by males (Knowlton 1979). By reproducing in synchrony females increase the male costs of brood abandonment or cannibalization. Unfortunately the data were not sufficient to test the hypotheses generated by this model, as evidenced by the sensitivity of the correlation analysis to site definition. It is still worth looking into, but it is necessary to use more sites, define sites based on the behavior of females, and measure spawning by females.

## Reproductive Synchrony in Other Damselfishes

The spawning date synchrony index was broadly applicable to damselfishes. Choosing the window size for searching for synchronous spawning dates was difficult, especially for species that showed little synchrony and had short time series, and for _Stegastes dorsopunicans_ which had overlapping broods. It makes biological sense that window sizes should be based on the number of days of brood care and on cycling frequencies, and that these different windows measure different things. The biological and environmental factors producing synchronization may be different for the time scales of brooding and larger time scales. These different measures of synchrony may prove useful in analyzing the importance of these factors. For instance, the effect of food availability on brood-level synchrony versus lunar-level synchrony could be determined using different window sizes.

This analysis was designed to demonstrate how to quantify synchrony, test its significance, and to provide data to interpret the evolution of synchrony in _D. albisella_. It is clear that there are other issues to investigate including how synchronization changes over time, as evident in _Abudefduf saxatilis_ and _Chromis notata_ (Figure 3).

## Phylogenetic Constraints on Reproductive Synchrony

If there is selection against reproductive synchrony, why does _D. albisella_ spawn in synchrony? _D. albisella_ is among the most derived species in its genus (Godwin 1995, DM unpublished data). All other _Dascyllus_ species that have been investigated appear to spawn in synchrony, although there is no published data that could be used to calculate the level of synchrony of these species. Even though _D. albisella_ shows high levels of synchronization, it may be lower than other _Dascyllus spp._

Current taxonomic organization places _Chromis_ as the sister-genus to _Dascyllus_ (Allen 1991). All _Chromis_ species for which there are data have been said to spawn in synchrony, although the data are not always given and _Chromis notata_ is not as

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synchronous as D. albisella. However, some taxonomists feel that Amphiprion is the true sister-genus to Dascyllus, because D. albisella juveniles seek shelter in anemones and because they also change sex (Les Kaufman and John Godwin, personal communications). Amphiprion is monogamous, but a female will share an anemone with several males, and does not spawn in synchrony (Fricke and Fricke 1977, this study).

What story we tell about the evolution of synchrony will differ depending on which is the true sister-genus. If it is Chromis, then synchrony may have evolved in these planktivorous fishes in response to selection pressures to reduce the time lost feeding in the water column due to reproduction. If Amphiprion is the true sister genus, then synchrony may have been lost in Amphiprion or evolved as part of the haremic lifestyle of the common ancestor of the Dascyllus genus, and although D. albisella is not haremic it still spawns in synchrony. Even when this phylogenetic uncertainty is resolved, it will be necessary to determine the effect of spawning synchronization on larval survivorship to fully understand the evolution of synchrony.

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Table 1. P-values of randomization test using the correlation method to test for greater synchrony within sites than between.

| | HO | WE | B14-1 | B14-2 | B14-3 |
|---|---|---|---|---|---|
| HO | | 0.000 | 0.000 | 0.750 | 0.008 |
| WE | | | 0.003 | 0.037 | 0.111 |
| B14-1 | | | | 0.000 | 0.000 |
| B14-2 | | | | | 0.065 |
| B14-3 | | | | | |

Table 2. P-values of randomization test using the correlation method to test for greater synchrony within sites than between, with a subset of fish in the first three sites.

| | HO | WE | B14-1 | B14-2 | B14-3 |
|---|---|---|---|---|---|
| HO | | 0.01 | 0.10 | 0.44 | 0.11 |
| WE | | | 0.00 | 0.10 | 0.00 |
| B14-1 | | | | 0.00 | 0.00 |
| B14-2 | | | | | 0.19 |
| B14-3 | | | | | |

Table 3. P-values of randomization test using the spawning date method to test for greater synchrony within sites than between.

| | HO | WE | B14-1 | B14-2 | B14-3 |
|---|---|---|---|---|---|
| HO | | 0.62 | 0.00 | 0.24 | 0.14 |
| WE | | | 0.01 | 0.37 | 0.52 |
| B14-1 | | | | 0.00 | 0.00 |
| B14-2 | | | | | 0.02 |
| B14-3 | | | | | |

Table 4. P-values of randomization test using the spawning date method to test for greater synchrony within sites than between, with a subset of fish in the first three sites.

| | HO | WE | B14-1 | B14-2 | B14-3 |
|---|---|---|---|---|---|
| HO | | 0.01 | 0.00 | 0.01 | 0.01 |
| WE | | | 0.00 | 0.12 | 0.04 |
| B14-1 | | | | 0.00 | 0.00 |
| B14-2 | | | | | 0.03 |
| B14-3 | | | | | |

Table 5. Comparison of synchrony measures using correlation and spawning date methods for each site in April.

| Site | Correlation Synchrony | Correlation Method Rank | Spawning Date Synchrony | Spawning Date Rank |
|---|---|---|---|---|
| HO | 0.39 | 5 | 0.85 | 5 |
| WE | 0.65 | 1 | 0.69 | 4 |
| B14-1 | 0.58 | 2 | 0.22 | 1 |
| B14-2 | 0.55 | 3 | 0.42 | 3 |
| B14-3 | 0.41 | 4 | 0.39 | 2 |
| HO subsite | 0.42 | | 0.23 | |
| WE subsite | 0.86 | | 0.19 | |
| B14-1 subsite | 0.61 | | 0.09 | |

Table 6. Correlation between percent of males receiving clutches and clutch size.

| Site | Spearman Rank Correlation | p-value | n |
|------|---------------------------|---------|---|
| HO | -0.007 | 0.986 | 10 |
| WE | -0.354 | 0.235 | 13 |
| B14-1 | 0.406 | 0.216 | 11 |
| B14-2 | -0.491 | 0.179 | 9 |
| B14-3 | -0.302 | 0.467 | 8 |
| | | | |
| HO subsites | 0.000 | 1.000 | 4 |
| WE subsites | -0.395 | 0.381 | 7 |
| B14-1 subsites | 0.700 | 0.188 | 5 |

Table 7. Comparison of premature brood loss and non-developing (bad) broods on synchronized (synch) and unsynchronized (unsynch) days. Data for sites and subsites are shown separately.

| Site | Spawnings on Synch Days | Spawnings on Unsynch Days | Spawns on Synch Days with Bad Brood* | Premature Loss. on Synch Days | Spawns on Unsynch Days with Bad Brood* | Premature Loss Unsynch Days |
|---|---|---|---|---|---|---|
| HO | 15 | 10 | 1 | 1 | 0 | 0 |
| WE | 21 | 13 | 2 | 0 | 0 | 1** |
| B14-1 | 26 | 8 | 8 | 2 | 3 | 0 |
| B14-2 | 17 | 9 | 3 | 0 | 1*** | 1*** |
| B14-3 | 16 | 7 | 4 | 2 | 1 | 0 |
| Total | 95 | 47 | 18 | 5 | 5 | 2 |
| Percent | | | 18.9% | 5.3% | 10.6% | 4.3% |
| | | | | | | |
| HO subsite (n=5) | 14 | 3 | 1 | 1 | 1 | 0 |
| WE subsite (n=6) | 21 | 5 | 0 | 0 | 0 | 0 |
| B14-1 subsite (n=8) | 21 | 1 | 5 | 2 | 0 | 0 |

\* ≥1/2 of brood not developing
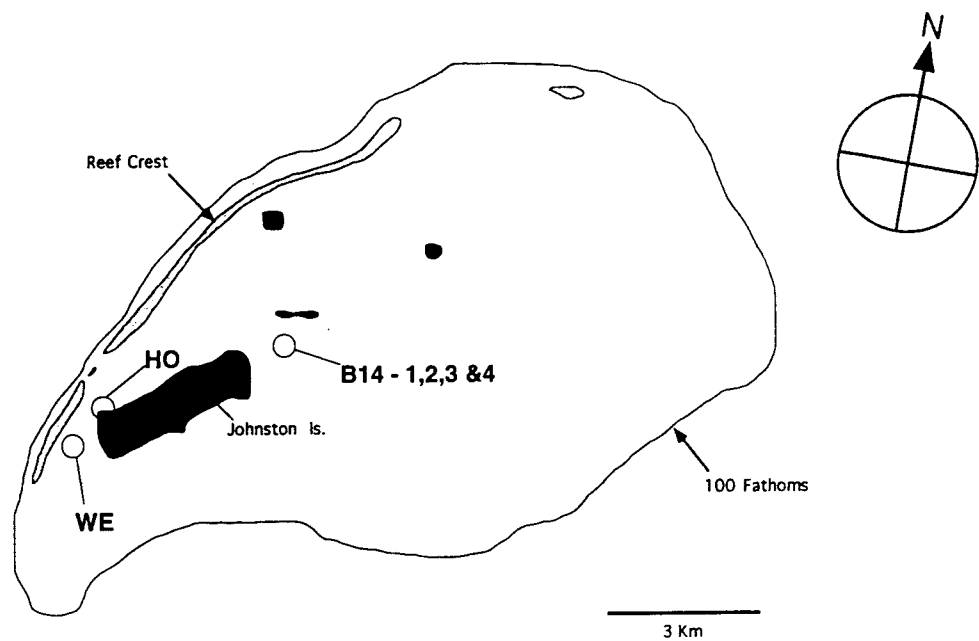\*\* Brood eaten after male disappeared, probably eaten
\*\*\* Same nest, premature disappearance of bad eggs

Table 8. Autocorrelations and spawning date method synchrony indices for damselfishes scaled by the "unsynchronized" index. Larger indices are more synchronized. Three sets of synchrony indices are given using different window lengths to search for dates of synchronized spawning: number of days brooding until hatch -1, maximum autocorrelational lag (i.e. period)/2, and the window that results in the maximum synchrony score. P-values are the results of randomization tests with 100 randomizations, and indicate whether spawning was significantly different than random for a given window length. * This was the only synchrony window that showed spawning synchronization was statistically significant for __Amphiprion clarkii__.

| Species | Autocorrelation Lag | Autocorrelation r | Brooding-1 Window | Brooding-1 Synchrony Index | Brooding-1 p-value | Period/2 Window | Period/2 Synchrony Index | Period/2 p-value | Max Index Window | Max Index Synchrony Index | Max Index p-value | Reference |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Chrysiptera cyanea | 7 | 0.581 | ? | - | - | 3 | 1.103 | 0.55 | 6 | 1.500 | 0.02 | Thresher and Moyer, 1983 |
| Chrysiptera rollandi | 2 | 0.220 | ? | - | - | 2 | 1.078 | 0.49 | 11 | 1.168 | 0.00 | Thresher and Moyer, 1983 |
| Chrysiptera biocellata | 16 | 0.351 | ? | - | - | 8 | 1.235 | 0.00 | 14 | 2.161 | 0.00 | Thresher and Moyer, 1983 |
| Pomacentrus chrysurus | 14 | 0.646 | 3 | 1.127 | 0.00 | 7 | 1.164 | 0.00 | 13 | 2.114 | 0.00 | Doherty, 1983 |
| Stegastes dorsopunicans | 30 | 0.141 | 3 | 1.125 | 0.00 | 15 | 0.865 | 0.04 | 2 | 1.951 | 0.00 | Petersen and Hess, 1991 |
| Microspathodon chrysurus | 28 | 0.708 | 5 | 1.010 | 0.06 | 14 | 0.979 | 0.03 | 25 | 1.748 | 0.00 | Pressley, 1980 |
| Amphiprion clarkii | 28 | 0.284 | 8 | 0.840 | 0.51 | 14 | 0.941 | 0.11 | 2 | 1.375 | 0.23 | Ochi, 1985 |
|  |  |  |  |  |  |  |  |  | 6 | 1.044* | 0.05 |  |
| Chromis notata: 1981 | 11 | 0.203 | 5 | 1.084 | 0.00 | 5 | 1.084 | 0.00 | 12 | 1.371 | 0.00 | Ochi, 1986 |
| Chromis notata: 1982 | 8 | 0.307 | 5 | 0.872 | 0.12 | 4 | 0.835 | 0.31 | 9 | 1.090 | 0.00 | Ochi, 1986 |
| Abudefduf saxatilis | 7 | 0.408 | 4 | 0.906 | 0.21 | 3 | 1.022 | 0.20 | 63 | 1.371 | 0.00 | Foster, 1987 |
| Abudefduf troschelii: Jul | - | - | 3 | 2.594 | 0.00 | - | - | - | 5 | 4.324 | 0.00 | Foster, 1987 |
| Abudefduf troschelii: Oct | - | - | 3 | 2.464 | 0.00 | - | - | - | 4 | 3.286 | 0.00 | Foster, 1987 |
| Abudefduf troschelii: Nov | - | - | 3 | 3.536 | 0.00 | - | - | - | 5 | 5.893 | 0.00 | Foster, 1987 |
| Dascyllus albisella: Hawaii | 5 | 0.716 | 3 | 2.223 | 0.00 | 2 | 1.677 | 0.00 | 5 | 3.714 | 0.00 | Danilowicz, 1985a |
| Dascyllus albisella: HO | 6 | 0.401 | 3 | 1.300 | 0.31 | 3 | 1.300 | 0.31 | 2 | 2.600 | 0.02 | This Study |
| Dascyllus albisella: WE | 6 | 0.820 | 3 | 2.250 | 0.00 | 3 | 2.250 | 0.00 | 3 | 2.250 | 0.00 | This Study |
| Dascyllus albisella: B14-1 | 6 | 0.741 | 3 | 3.188 | 0.00 | 3 | 3.188 | 0.00 | 6 | 4.636 | 0.00 | This Study |
| Dascyllus albisella: B14-2 | 6 | 0.579 | 3 | 1.773 | 0.03 | 3 | 1.773 | 0.03 | 6 | 3.545 | 0.00 | This Study |
| Dascyllus albisella: B14-3 | 5 | 0.562 | 3 | 1.917 | 0.01 | 2 | 2.300 | 0.06 | 5 | 3.194 | 0.00 | This Study |
| Dascyllus albisella: HO subsite | 6 | 0.356 | 3 | 1.950 | 0.14 | 3 | 1.950 | 0.14 | 2 | 6.500 | 0.01 | This Study |
| Dascyllus albisella: WE subsite | 6 | 0.861 | 3 | 3.900 | 0.00 | 3 | 3.900 | 0.00 | 6 | 7.800 | 0.00 | This Study |
| Dascyllus albisella: B14-1 subsite | 6 | 0.807 | 3 | 8.250 | 0.00 | 3 | 8.250 | 0.00 | 6 | 16.500 | 0.00 | This Study |

Figure 1. A. Map of Johnston Atoll. B. Map of coral heads with males and/or females used in this study. Lines connecting dots indicate patterns of female movement during visting behavior. Dots enclosed by ovals represent coral heads of the males used as subsites.

# A.



Reef Crest

HO

B14 - 1,2,3 &4

Johnston Is.

WE

100 Fathoms

N

3 Km

# B.

Herbicide Orange

Shore

West End

Buoy 14

B14-1

B14-2

B14-3

Meters

199
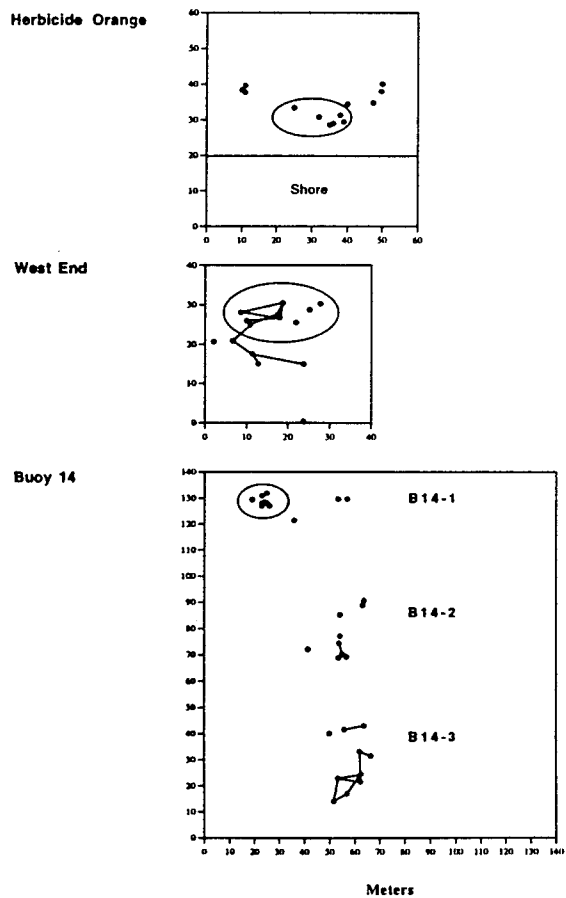
Figure 2. Time series of the number of broods received per day at each site. A. July 1993. B.

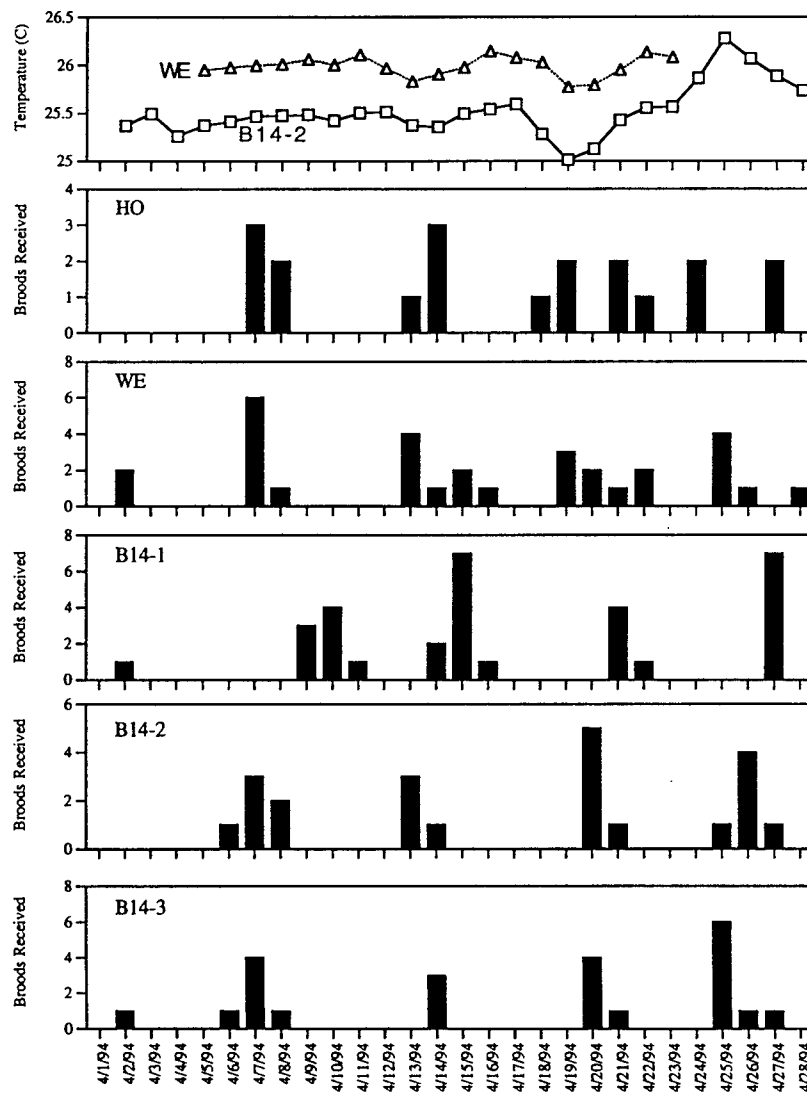April 1994 with water temperature at WE and B14-2.
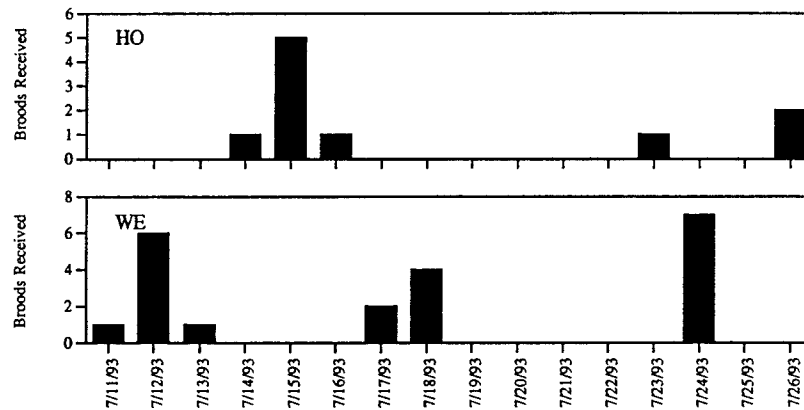
Figure 3. Time series of spawning for damselfishes drawn from the literature (see Table 8 for references), and "unsynchronized" and random time series.
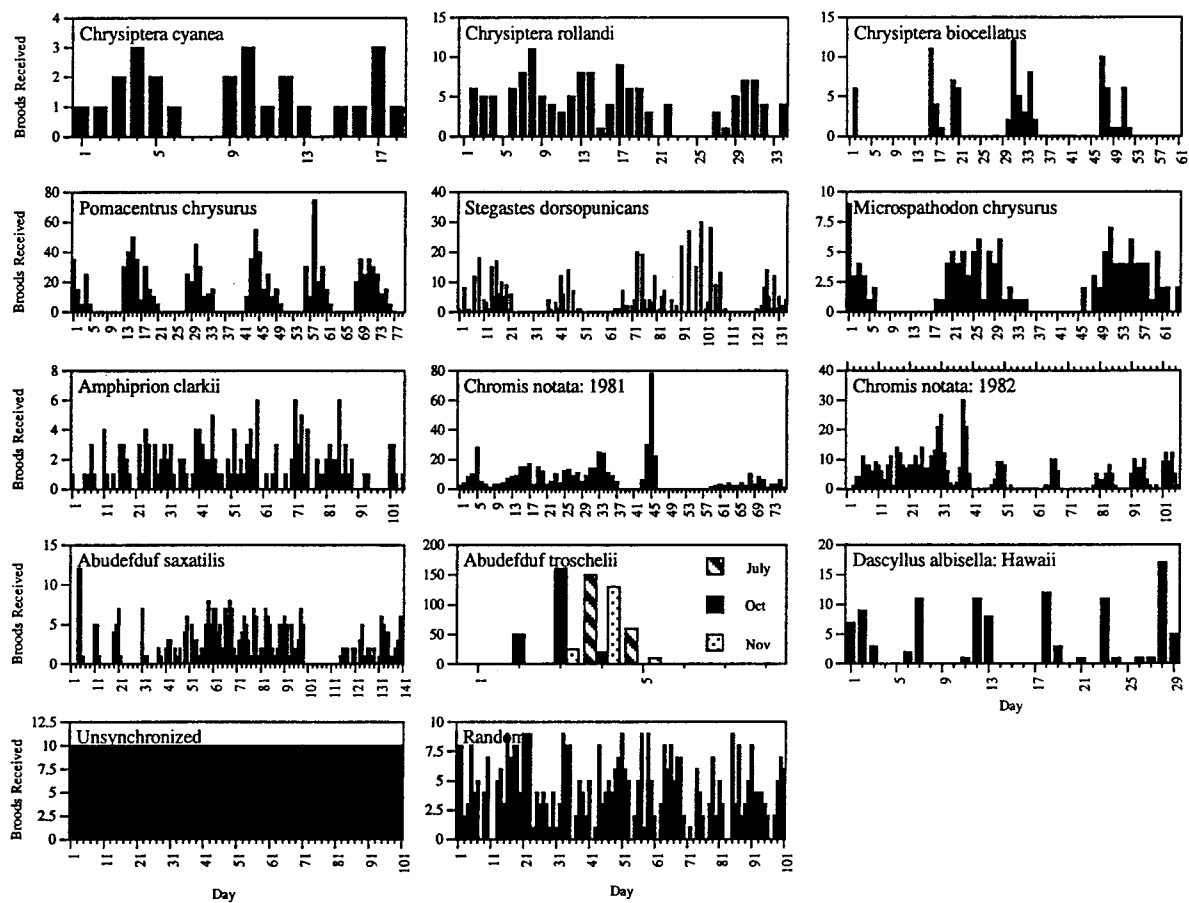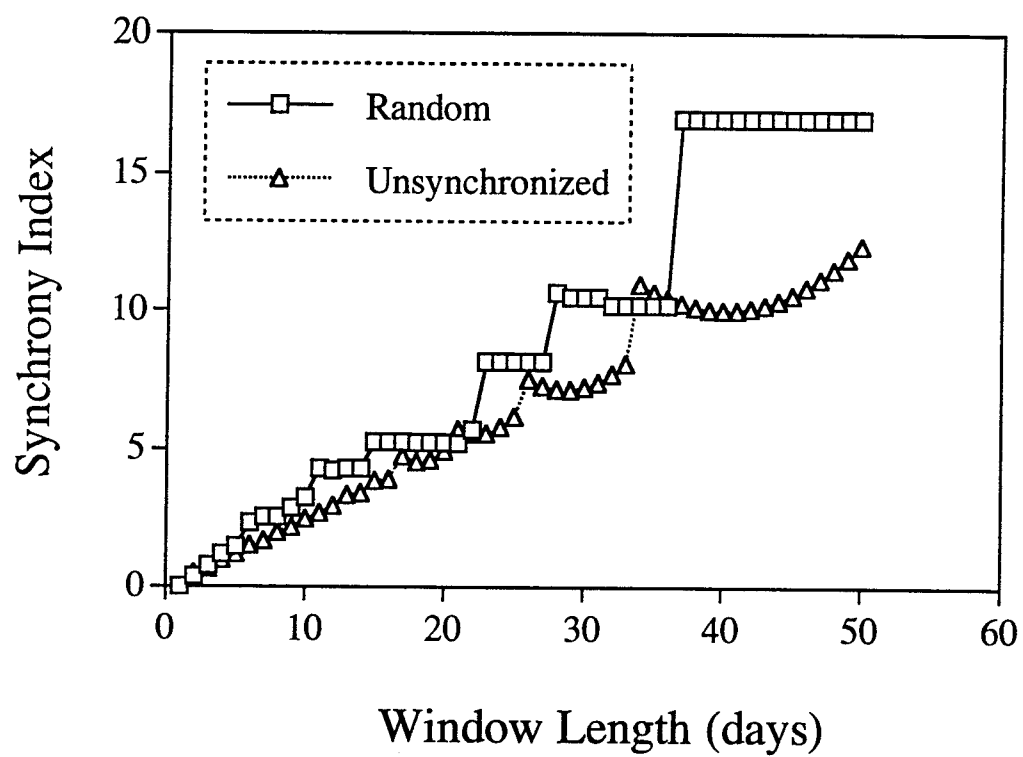
Figure 4.  Spawning date method synchrony index versus window length for "unsynchronized" and random time series.

# Chapter VII    Conclusions

"It is good to know what you are doing. The man with his pickled fish has set down one truth and has recorded in his experience many lies. The fish is not that color, that texture, that dead, nor does he smell that way."
--John Steinbeck. The Log from the Sea of Cortez

The sounds produced by the damselfish <u>Dascyllus albisella</u>, and most likely other damselfishes and cichlids, are simple pulsed sounds that act over short distances (<10 m) with the most robust information encoded in the pulse period. It is difficult to demonstrate the role of sounds in mate choice and reproductive synchrony. It appears that calling rate is used by females to choose mates, and it is unlikely that other aspects of the variation in the sound are detectable by females, or are too modified by the environment to be transmitted reliably.

Reproduction is highly synchronized, and the distances over which synchrony exists are consistent with the distances over which acoustic signals are detectable. Furthermore, there is a correspondence between calling rate and reproduction. However, these are correlations that do not rule out the action of other factors including visual stimuli and chemical communication. It has been hypothesized and there are experimental data that indicate that females can decrease the probability males will abandon clutches by spawning in synchrony (Knowlton 1979, Petersen and Hess 1991). This prediction should lead one to focus on the behavior of the females, as opposed to the males which we are so keen to observe.

The visiting behavior of females is intriguing. They perform a pseudo-spawning behavior during visiting, but what information are they gaining about a prospective mate? I propose two hypotheses, which are not mutually exclusive. First, they may be able to determine the size of the males nest and how many eggs it could hold. Second, they may inspect the 'quality' of the nest. Although, we all claim that in the preparation of nests males are cleaning off debris, there is no data on what is changing as the male prepares the nest and thus what 'quality' may be.

If females choose mates based on courtship rates, rather than any particular feature of the courtship sound, sexual selection would not be a potent force in contemporary signal evolution.

Sexual selection for high courtship rates would be selecting for a variable that is largely environmentally determined by the energy available to the male. Courtship rates might provide females with an honest signal of the ability of a male to care for and defend a clutch of eggs.

Pulse period discrimination in fishes is not particularly acute. Goldfish can only detect 10 msec changes in pulse periods of 40 msec. Data on species-specific call discrimination in four closely related damselfishes support a somewhat better ability (5 msec); while they can discriminate the calls of other species to some degree, there is considerable overlap in their responses to conspecific and heterospecific calls (Spanier 1979). If this is generally true of damselfishes and cichlids, there is not much room for meaningful species-specific variation. Species-specific pulse rates would have to act in concert with other call features such as pulse number, and other species-specific cues such as color. It is clear that we need much more data on the ability of damselfishes to detect sounds and discriminate variation in pulse number and pulse period.

The courtship sound of D. albisella appears the same as that of its sister species D. trimaculatus from both the Red Sea (Israel) and the Pacific Ocean (Japan), suggesting that the evolution of new sounds can be quite slow compared to insects and frogs (Ewing 1989; Cocroft and Ryan 1995). The Dascyllus genus provides an excellent opportunity to investigate the evolution of acoustic signals in damselfishes. Each of the three Dascyllus complexes (D. aruanus, D. reticulatus, and D.trimaculatus) has one cosmopolitan species and at least one isolated species. This genus provides the opportunity to investigate the signals of sympatric species. In the Red Sea D. marginatus and D. aruanus share coral heads but do not interbreed (Shpigel and Fishelson 1986). Only the species with the dominant male will reproduce. Courtship sounds could play an important role in the reproductive isolation of these species.

How did the signal jump and its associated sound evolve? Of the Labroidei, the most prolific sound-producers, the damselfishes (Pomacentridae) and the cichlids (Cichlidae), have male parental care of demersal broods. The wrasses (Labridae) and parrotfishes (Scaridae) are, for the most part, spawners of pelagic eggs with no parental care, and surfperches (Embiotocidae) have internal fertilization. Females of demersally spawning species could gain greater reproductive

fitness if there was variation in the parental abilities of males that they could detect. The signal jump could provide a reliable cue, and probably evolved through the good-parent process of sexual selection (Hoelzer 1989).

The signal jump is superficially similar to the spawning rushes of the labrids, in which fish swim rapidly up to spawn high in the water column, and then rapidly back down. Whether it is a relic of the spawning rush, or an independently derived behavior will be difficult to determine. It is also difficult to say whether the sound came before, at the same time, or after the signal jump. The sound may have grown out of aggressive interactions, since other labroids are known to make sounds in aggressive situations. The combination of the signal jump with sound makes it easy for the diver, and presumably the fish, to identify the calling male.

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# Appendix I


# SPAWNING SOUNDS OF THE DAMSELFISH, <u>DASCYLLUS ALBISELLA</u> (POMACENTRIDAE), AND RELATIONSHIP TO MALE SIZE

# ABSTRACT

Synchronous audio-video recordings were made of free-living <u>Dascyllus</u> <u>albisella</u> on coral reefs at Johnston Atoll, Central Pacific Ocean. Males produced distinct and consistent sounds during courtship and mating. The courtship sound is a well-known feature of pomacentrid behavior, and is produced during the signal jump. Male <u>D.</u> <u>albisella</u> also produced a mating sound, which has not been previously described for any other pomacentrid. The mating sound is produced as the male quivers during spawning. The courtship sound differed from the mating sound by having a greater number of pulses ($6\pm4$ vs. $3\pm1$, mean SD), a longer duration ($262\pm57$ vs. $127\pm45$ msec), and a faster pulse rate ($57\pm5$ vs. $63\pm11$ msec/pulse). The courtship sounds of larger males were lower in frequency than those of smaller males ($r^2=0.64$, power regression). The median dominant frequency of small males (20 to 40 g) was 390 Hz (n=12 males), compared to 334 Hz (n=7 males) for large males (40 to 60 g).

# INTRODUCTION

Males of many fishes, including pomacentrids, produce sounds during courtship. The simplest information that may be contained in the acoustic signals are the male's location, readiness to spawn, and body size. In this study we examined the courtship calls of <u>Dascyllus albisella</u> (Pomacentridae), to define within- and between-individual variation in pulse content and dominant frequency. We also discovered that <u>D. albisella</u> produced another pulsed sound that was associated with the mating act. The details of these acoustic signals were examined to determine if they were distinct and definable according to behavioral context, and whether any features of the courtship call were related to male size.

A basic principle of underwater physics is that larger swimbladders resonate at lower frequencies than smaller swimbladders (Clay and Medwin 1977, Urick, 1983). In sonic fishes, this association may provide females with a reliable signal of male size. Body size is an important variable affecting the reproductive success of males in many fishes (Perrone 1978, Noonan 1983, McKaye 1986, Myrberg et al. 1986, Hert 1990, Wooton 1990, Bisazza and Marin 1991, but see Petersen 1995). There is some evidence that among sonic teleosts (except, perhaps, for those species with highly specialized sonic muscles on the swimbladder) larger fish produce lower frequency sounds than smaller fish (Myrberg et al. 1965, Demski et al. 1973, Fine et al. 1977, Rowland 1978, Myrberg and Riggio 1985). To date this has only been rigorously tested for the bicolor damselfish, <u>Stegastes partitus</u> (Pomacentridae) (Myrberg et al. 1993) We hypothesize that frequency is largely a morphologically determined signal related to swimbladder and body size, and therefore should be evident among many species.

# METHODS

## Study Site

Johnston Atoll is a coral reef ecosystem in the Central Pacific Ocean (16° 44' N, 169° 31' W). Recordings were made of free-living fish in the lagoon during May 1991 and April 1994. Sea water temperatures in the lagoon ranged from 26.0 to 26.8° C in May 1991, and 25.1 to 26.6° C in April 1994. Water depth was between 4-6 m.

## Acoustic-Video Recording

Synchronous audio-video recordings were made underwater using a SONY model V-9 8mm video camera coupled to a hydrophone. The hydrophone had a frequency range of 10 to 3000 Hz and a sensitivity at 10 psi of -162 dBV/mPa ± 2dB (BioAcoustics, Box 594, Woods Hole, MA).

Audio-video recordings of courting and mating <u>Dascyllus albisella</u> were made while using SCUBA with controlled breathing to avoid excessive regulator and bubble noise. The hydrophone was generally placed between 0.5-1.0 m of the fish, while the diver was positioned 3 to 5 m away operating the video camera. The hydrophone was attached to the video camera by a 5 m long cable and manipulated on a sound boom (a 2.5 m pole) that was rested on the bottom. The hydrophone was located at the end of the boom with 40 cm of free cable, and buoyed so it floated freely in the water column. After recording, fish were collected by spear and measured and weighed while fresh. Histological analysis of the gonads of the 9 males recorded in May 1991 confirmed that each specimen was a mature male.

## Acoustic Analysis of Sounds

Each sound was classified according to the behavior of the male producing the sound as seen on the video. Acoustic analyses used the signal processing hardware and software package SIGNAL (Engineering Design, Belmont, MA). The acoustic signal was processed through a digital filter (Frequency Devices, Model 9002) that attenuated frequencies above 2 kHz (after verifying that the dominant energy in the signals was below 1 kHz), before being converted to a digital signal at a sampling rate of 5000 Hz. Dominant frequency was analyzed using 325 recordings from 19 males (mean=17 sounds/fish, range=5-44). Other analyses of courtship sounds used 393 calls from 25 males (6 males were not collected) (mean=15 calls/fish, range=4-44). Measurements of the number of pulses in a sound and its duration were made from the oscillogram. Pulse period was calculated by dividing the call duration in milliseconds by the number of pulses minus one in that call. The dominant frequency of a call was calculated by averaging the dominant frequencies of the pulses comprising the call. Since the sounds produced by D. albisella are broad-band, energy is spread among several frequencies and not concentrated at one frequency as in tonal sounds. To calculate the dominant frequency of a sound, each pulse within a multiple-pulse sound was isolated, and its power spectrum was derived by a 32k-point fast fourier transform (FFT). The power spectrum displays the distribution of energy in the signal as a function of frequency. The dominant frequency of a pulse was calculated from the power spectrum by measuring 3 dBV down from the peak frequency, and averaging the lowest and highest frequencies at that amplitude. By determining the dominant frequency of a pulse using this "3dB down" technique, the average of the energy distribution is better represented than by the frequency that has the peak energy (R. Fricke, M.I.T., Cambridge, MA, pers. comm.). Because the signal lengths of the pulses were about 50 ms, the frequency resolution bandwidth is approximately 20 Hz (Papoulis 1984).

Statistical analyses used StatWorks (Cricket Software, Philadelphia, PA) and SYSTAT (Systat Inc, Evanston, IL). For comparison of correlation coefficients (r) the

95% confidence intervals for the linear regression and power regressions were calculated using Fisher's z-transformation (Zar 1984).

We followed the nomenclature of Allen (1991) for the pomacentridae: Stegastes partitus synonyms are Pomacentrus partitus and Eupomacentrus partitus.

## RESULTS

### Courtship and Mating Sounds

Males produced the courtship call while performing the "signal jump" or "dip", in which a male rises in the water column and then rapidly swims down while producing the pulsed courtship sound (described by Myrberg (1972), for Stegastes partitus) (Figure 1 a). In addition to the courtship sound, males also produced a mating sound. This mating sound was accompanied by a "mating quiver", a lateral quivering of the body that began at the head and progressed posteriorly (Figure 1b). Analysis of videos of six males performing this behavior revealed that it occurred at the beginning of mating bouts as a female moved to the nest site, and during what we presumed to be egg laying. The male apparently fertilized the eggs while fanning the nest surface both during and after egg laying. The mating quiver did not occur during apparent male fertilization behavior.

The number of pulses of the courtship calls (n=393 by 25 males) correlated well with the call duration (r=0.841, p<0.001), indicating that the courtship calls had a relatively constant pulse period. Coefficients of variation were calculated for courtship calls using the median values of the call characteristics for each male (frequency CV= 10%, number of pulses CV=10%, call duration CV=12%, pulse period CV=9%).

Two-way ANOVA analyses were used to test for differences in call characteristics (number of pulses, call duration, and pulse period) between courtship calls and mating sounds using call type (n=2) and individual males (n=6) as factors. The analysis of pulse

period excluded sounds with only one pulse. The sound made during the mating quiver had a longer pulse period (mean±SD=63±11 msec/pulse) than the courtship call (mean±SD=57±5 msec/pulse), was of shorter duration (mean±SD=127±45 msec vs. mean±SD=262±57 msec), and contained fewer pulses (mean±SD=3±1 vs. mean±SD=6±4) (Figure 2). All of these differences were highly significant (p<0.001). However, there was a significant interaction between call type and individual male for pulse period, thus this difference can not be considered statistically significant.

## Relationship of Courtship Call and Male Size

To determine if the size of the fish producing the courtship calls could explain any of the variation in the call characteristics, the weights of the fish were plotted against the median number of pulses ($r^2$=0.147, p=0.094), duration ($r^2$=0.248, p=0.031), and period ($r^2$=0.096, p=0.148) (Figure 3). These analyses showed a positive slope indicating that the median number of pulses, call duration, and pulse period increased with increasing size. However, the $r^2$ values were low, indicating that much of the variation was not explained by the weight of the fish. Only duration had a slope significantly different than zero.

To test the hypothesis that the dominant frequency correlates negatively with male size, the medians of the dominant frequencies of the courtship calls were plotted against the weight of the fish and linear and power regressions were performed (Figure 4). These regressions produced a negative slope ($r^2$=0.590, p<0.001 linear, $r^2$=0.639, p<0.001 power), indicating that larger fish produced lower frequency calls. The correlation coefficients were not significantly different at ∝=0.05 (95% confidence intervals for linear regression, r=0.694±0.213; power regression, r=0.799±0.189). Among these fish, the mean coefficient of variation of the dominant frequency of the courtship calls was 11%±1% (mean±SD).

# DISCUSSION

The two sounds produced by <u>Dascyllus</u> <u>albisella</u> during courtship and mating are distinct in the number of pulses, duration of the sound, and pulse period. There is a negative relationship between male size and the dominant frequency of the courtship call; larger males produced lower frequency calls.

Although there is a lack of strong experimental data, most evidence suggests that sound is important in reproductive behavior of sonic fishes and plays a role in species and size identification (Myrberg 1980a, 1980b, 1981, Hawkins and Myrberg 1983). Playbacks of male courtship sounds elicited responses by both male and female conspecific pomacentrids (Spanier 1979, Myrberg and Spires 1972, 1980, Myrberg et al. 1986). Species-specific recognition of sympatric pomacentrids (<u>Stegastes</u> spp.) was experimentally demonstrated to be based upon the number of pulses and pulse rate of a call (Myrberg and Spires 1972, Spanier 1979). <u>D.</u> <u>albisella</u>, in comparison to <u>Stegastes</u> <u>partitus</u>, has a longer pulse period (45 msec vs. 38 msec) and more pulses per call (6 vs. 3). Its call is more similar to the call of <u>Stegastes</u> <u>dorsopunicans</u> (41 msec period, and 6 pulses per call) (data from Spanier 1979).

Can differences in call frequency be used by a female fish to evaluate male size or provide individual recognition of males? Non-ostariophysine fishes including, <u>Gobius</u> <u>niger</u> (Gobiidae), <u>Corvina</u> <u>nigra</u> (Sciaenidae), and <u>Sargus</u> <u>annularis</u> (Sparidae) can discriminate tones differing in frequency of about 10%; the frequency discrimination ability at 400 Hz is about 40 Hz for non-ostaryiophysine fishes (Fay 1988). If the discrimination ability of <u>D.</u> <u>albisella</u> is similar, then it could detect differences between males weighing 35g and 47g, which produce sounds of 375 Hz and 335 Hz, respectively (a 40 Hz difference). The ability of <u>D.</u> <u>albisella</u> to discriminate frequency differences of courtship

calls may be different than this example, because the discrimination tests were performed with tonal sounds, not broad-band pulsed sounds.

The association of specific sound patterns with courtship and mating behavior suggest that bioacoustic signals may be an important component of mate choice in D. albisella. Our results showing a size-dependent frequency of the courtship sound, and those of Myrberg (1993) for S. partitus, support the hypothesis that dominant frequency is morphologically determined by swimbladder and body size.

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Figure 1. A. Oscillogram (top) and spectrogram (bottom) of two courtship calls produced by one male Dascyllus albisella. B. Oscillogram and spectrogram of sounds produced during two mating quivers by the same individual as Figure 1a.
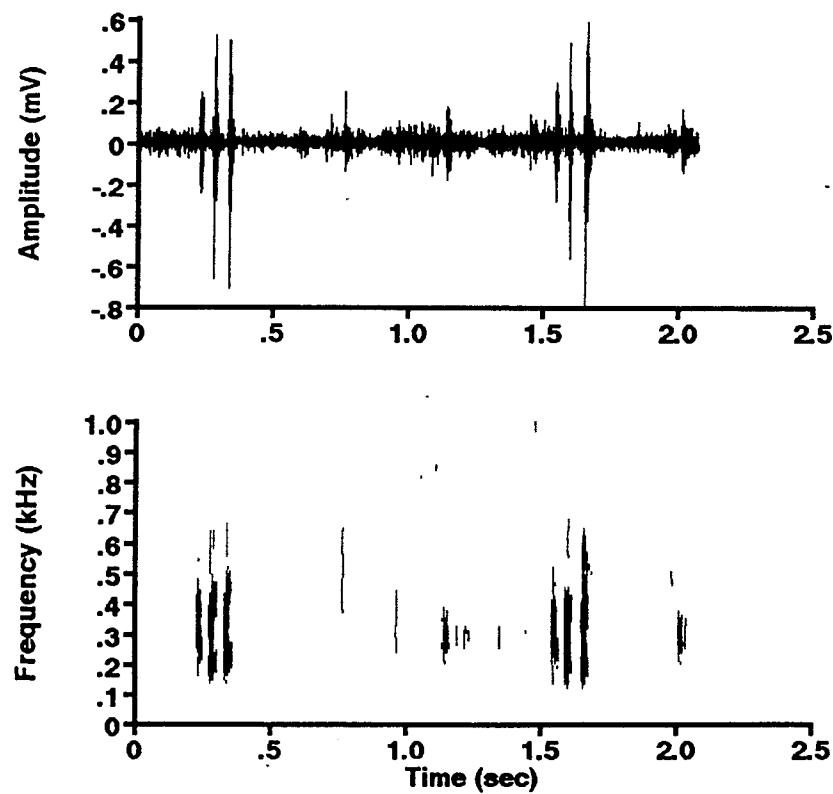
A.
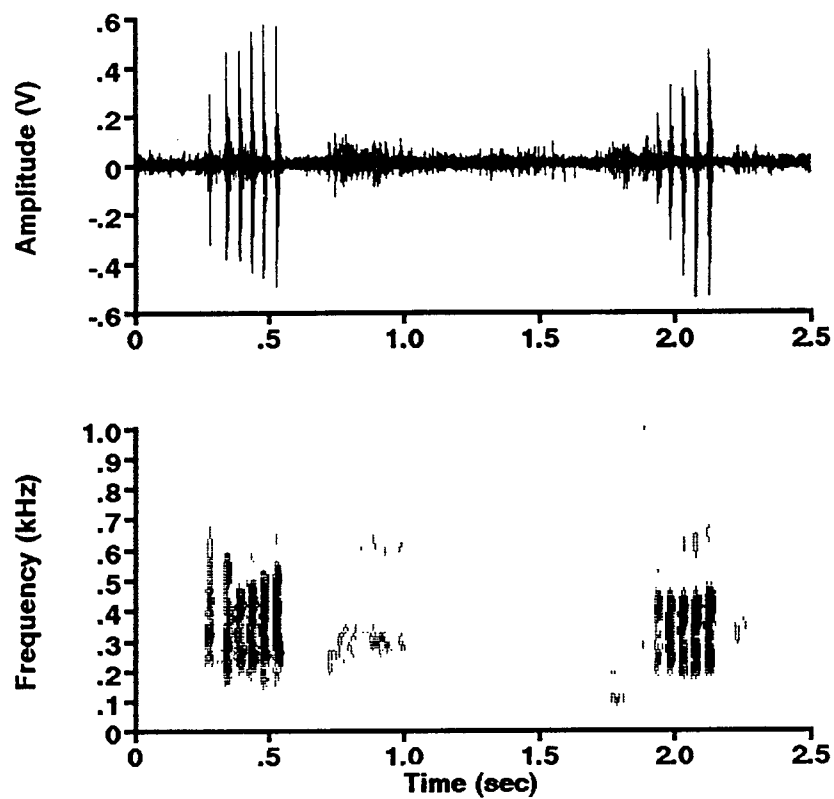
B.

Figure 2. Comparison of number of pulses versus duration for the sounds produced during the courtship dip and mating quiver. Each of the graphs is the data from one of six males.
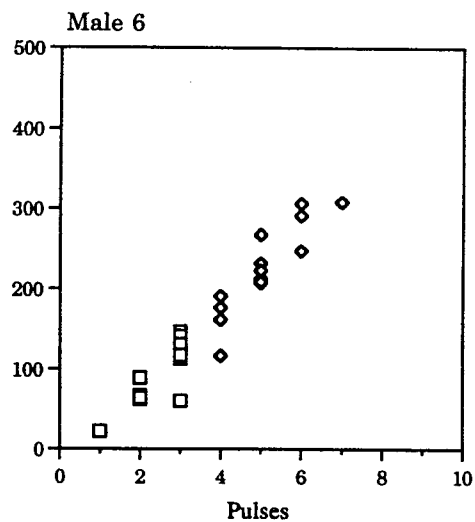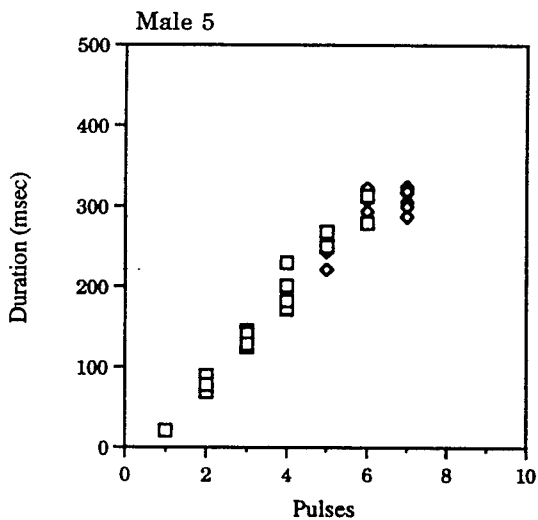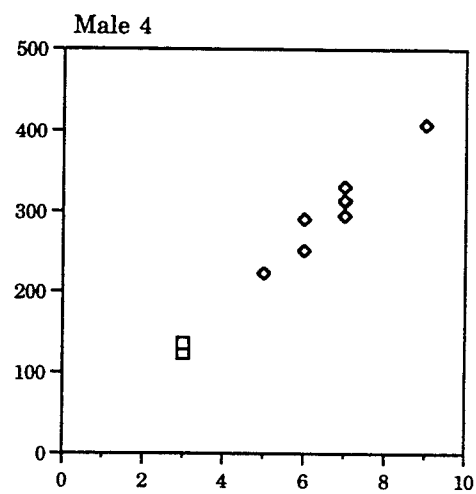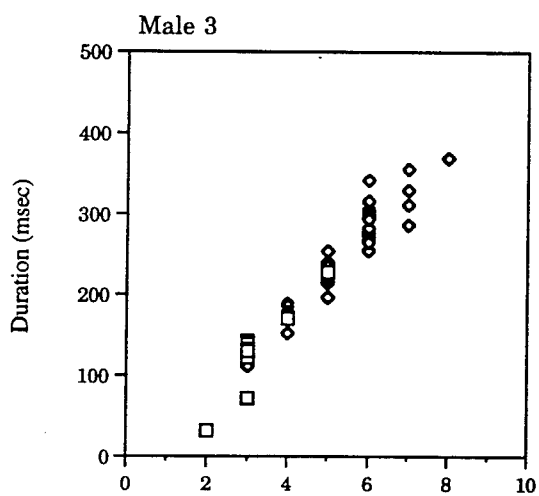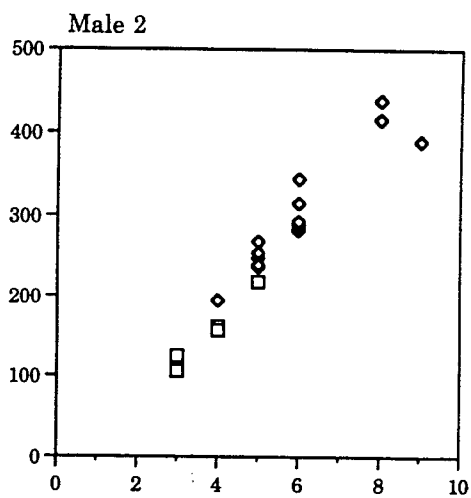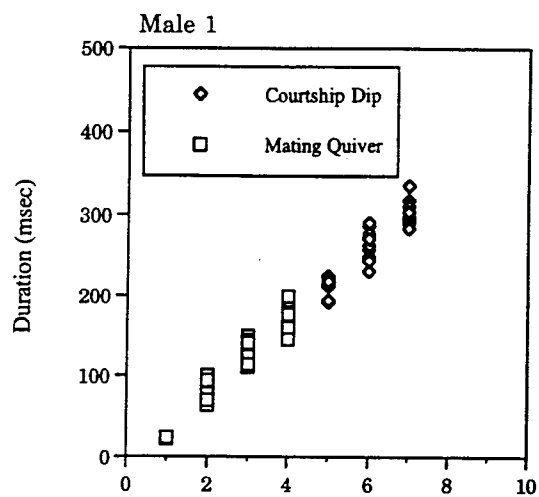
Figure 3. Relationships between male weight and three characteristics of the courtship sound. A. Number of pulses in a courtship call. B. Duration of a courtship call. C. Pulse period of the courtship calls. Squares represent the median value for an individual male with error bars showing the standard deviation. Median values are fitted with a linear regression and the equation for the regression is given above each graph.
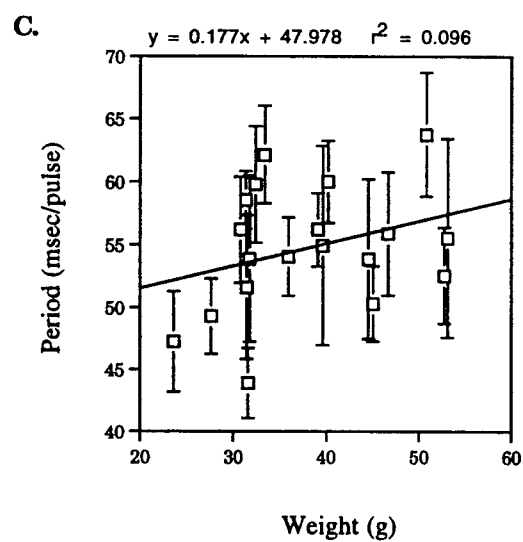
**A.**

y = 0.022x + 5.120    r² = 0.147

**B.**

y = 1.681x + 207.038    r² = 0.248

**C.**

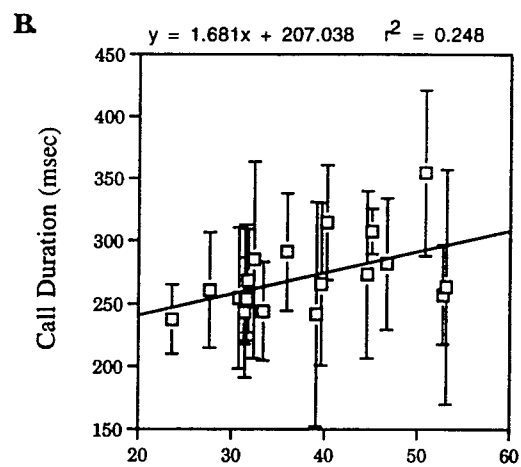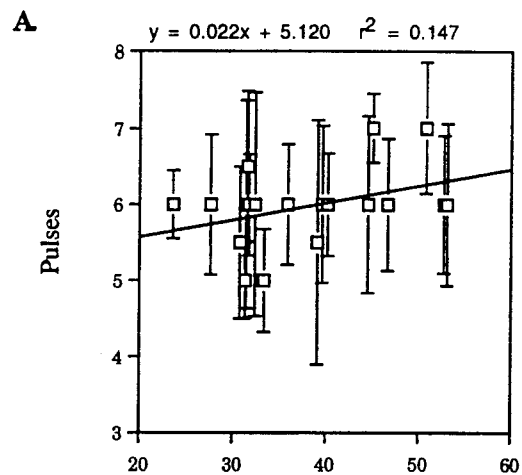y = 0.177x + 47.978    r² = 0.096

Weight (g)

Figure 4.  A.  Relationship between male weight and the dominant frequency of the courtship call.  Squares represent the median value for an individual male with error bars showing the standard deviation.  Median values are fitted with a linear regression and a power regression and the equations for the regressions are given above each graph.  B. Power spectra of one pulse from one courtship call for each of two males.  The dominant frequency of the pulse is indicated above the spectra.  The corresponding males that produced these sounds are labeled as 1 and 2 in Figure 4a.

**A.**
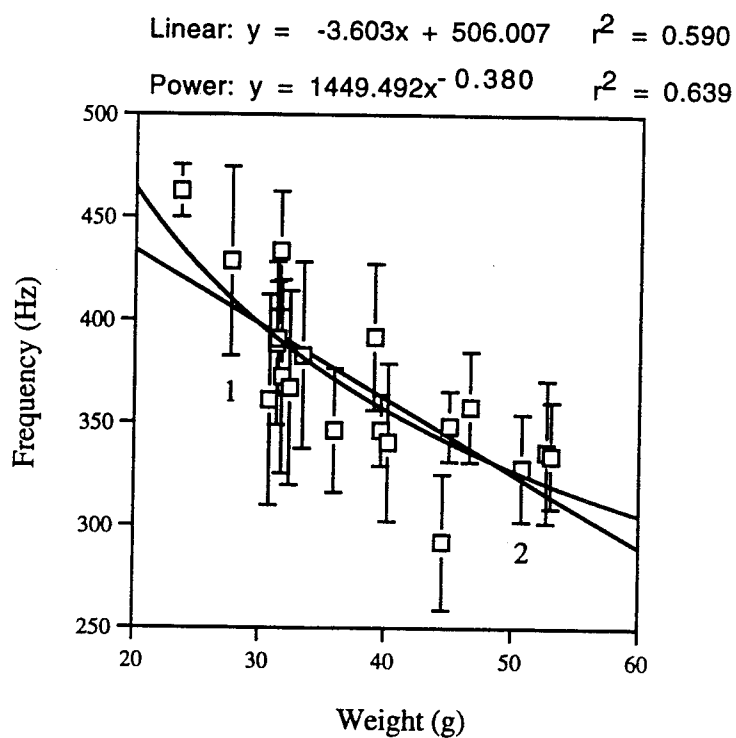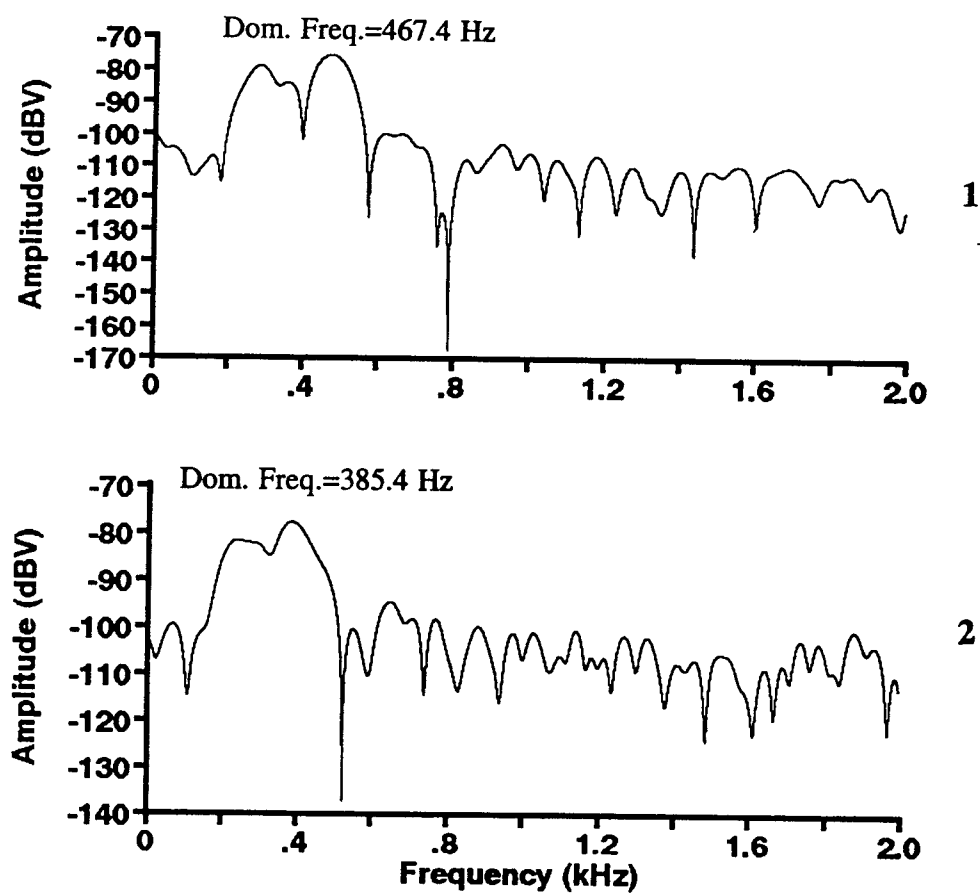
Linear: $y = -3.603x + 506.007$   $r^2 = 0.590$

Power: $y = 1449.492x^{-0.380}$   $r^2 = 0.639$



**B.**

Dom. Freq.=467.4 Hz

1

Dom. Freq.=385.4 Hz

2

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**16. Abstract (Limit: 200 words)**

This thesis is an intensive investigation of the sounds produced by the damselfish *Dascyllus albisella*, the effect of the environment on their acoustic signals, and how the sounds relate to reproduction.

*D. albisella* males produce pulsed sounds during the signal jump, visiting by females, mating, aggression, and nest preparation. Females make only aggressive sounds. There was no relationship between signal jump speed or distance with the number of pulses or pulse period of calls. The propagation analyses suggest that the courtship sound acts over short distances and that the pulse period provides the most reliable basis for signal detection.

A passive acoustic detection system was developed to continuously record sound production activity of individual males in the field. The rate of sound production could be used to determine the timing of spawning. Patterns of male reproductive success varied for individual males over successive reproductive cycles and was not correlated to male size. Rates of courtship were positively correlated with reproductive success for three males. Groups of isolated fish spawned in synchrony, but not in synchrony with other groups, even as close as 20-30m. Synchronization is likely based on social interactions and might develop through the courtship sounds.

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damselfish
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**b. Identifiers/Open-Ended Terms**

**c. COSATI Field/Group**

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